Canadian Special Publication of Fisheries and Aquatic Sciences 105

Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks

Edited by C. D. Levings, L. B. Holtby, and M. A. Henderson

Canada

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Resource Protection & Conservation
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DEPARTMENT OF FISHERIES AND OCEANS
OTTAWA 1989

89-05113/

Published by Publié par

Fisheries and Oceans Pêches et Océans

Communications Directorate Direction générale des communications

Ottawa K1A 0E6

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Available from authorized bookstore agents, other bookstores
or you may send your prepaid order to the
Canadian Government Publishing Centre
Supply and Services Canada, Ottawa, Ont. K1A 0S9

Make cheques or money orders payable in Canadian funds
to the Receiver General for Canada

A deposit copy of this publication is also available
for reference in public libraries across Canada.

Catalogue No. Fs 41-31/105E
ISBN 0-660-13232-X
ISSN 0706-6481

DFO/4174

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LEVINGS, C. D., L. B. HOLTBY, AND M. A. HENDERSON [ED.]. 1989. **Proceedings of the National Workshop on effects of habitat alteration on salmonid stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105: 199 p.**

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Abstract

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Participants in a National Workshop on Effects of Habitat Alteration on Salmonid Stocks were generally uneasy about our ability to make quantitative predictions regarding the effects of habitat changes on salmonid production. Fish habitat management was revealed as a complex business that must deal with an intrinsically variable resource living in an often unstable environment and harvested by a dynamic fishery. Habitat managers need the best possible information available to them and even then substantial judgement is needed to interpret data and make the best possible decision. Methodologies for predicting effects are becoming available through such techniques as linking life history models, an approach requiring long-term data sets consisting of many different variables for model development and verification. It was recommended that for each species of concern there should at least be an outline of a life history model which indicates stages sensitive to various habitat alterations to guide management actions. It was acknowledged that physical changes, including landscape effects and water quantity, are more easily measured than chemical effects, possibly because physical variables are usually measurable by standard engineering techniques. Chemical effects are more subtle and frequently the substances thought to be deleterious cannot be easily measured in the field. Sublethal effects may lead to increased mortality due to predation, disease, or food limitation and these effects are very difficult to evaluate for populations. With both physical and chemical effects, the consequences of the habitat changes must be assessed through a population model. Because of the current scientific difficulties in quantifying the effects of habitat change on salmonid populations, it appears that significant judgement or inference is required to interpret even major project data bases that deal with impacts on salmonid populations.

Résumé

LEVINGS, C. D., L. B. HOLTBY, AND M. A. HENDERSON [ED.]. 1989. Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105: 199 p.

Les participants à un atelier national sur les effets de l'altération de l'habitat sur les stocks de salmonidés étaient en général inquiets au sujet de notre capacité à faire des prévisions quantitatives concernant les effets des modifications de l'habitat sur la production de salmonidés. La gestion de l'habitat du poisson est complexe car on doit tenir compte d'une ressource intrinsèquement variable qui vit dans un milieu souvent instable et qui fait l'objet d'une pêche dynamique. Les gestionnaires de l'habitat ont besoin des meilleures informations possibles; même alors, il leur faut beaucoup de jugement pour interpréter les données et prendre la décision la meilleure possible. Les méthodes permettant de prédire les effets deviennent accessibles grâce aux techniques comme celle consistant à lier des modèles de cycle vital, une approche qui exige des séries de données à long terme comprenant un grand nombre de variables différentes qui aideront à élaborer et à vérifier les modèles. On a recommandé de donner au moins, pour chaque espèce présentant un intérêt, les grandes lignes d'un modèle de cycle vital qui indiqueraient les stades sensibles à diverses modifications de l'habitat afin de guider les gestionnaires. On a reconnu que les modifications physiques, y compris les effets sur le paysage et la quantité d'eau, sont mesurées plus facilement que les changements chimiques, probablement parce que les variables physiques sont habituellement mesurables par des techniques courantes de génie. Les effets chimiques sont plus subtils et il arrive souvent que les substances considérées comme nocives soient difficilement mesurables sur le terrain. Les effets sublétaux peuvent mener à une mortalité accrue causée par la prédation, la maladie ou la quantité limitée de nourriture et ces effets sont très difficiles à évaluer pour les populations. Les conséquences des modifications de l'habitat, qui ont des effets tant physiques que chimiques,

doivent être évaluées à l'aide d'un modèle de population. En raison des difficultés qu'ont actuellement les scientifiques à quantifier les effets de la modification de l'habitat sur les populations de salmonidés, il semble qu'il faille beaucoup de jugement ou d'esprit de déduction pour interpréter même les bases de données recueillies dans le cadre de grands projets qui portent sur les répercussions pour les populations de salmonidés.

Introduction

Before the era of widespread public concern for fish habitat, P.A. Larkin et al.(1959) wrote: "the development of British Columbia has been confined to such a recent period of history that it is relative easy to describe with some confidence the effects of man's activities on the abundance and distribution of freshwater species of fish". Almost 30 years later, many biologists would disagree with this statement because quantitatively contemporary ecology requires an ability to predict the effects of habitat alteration on fish production. Even now, however, inference and good scientific judgement, as displayed by Larkin et al. (1959), should not be discounted as a management tool but defensible management has to arise from scientific facts. The pressure for increased scientific understanding of how fish habitat influences fish production arises from a number of groups: (1) the fishing industry and fish stock managers who must decide on harvesting strategies to assure sustained fish production, (2) fish habitat managers, who have a mandate to guide the use of fish habitat so that sustained fish production is assured, and (3) industrial and resource developers, who are required by DFO policy to maintain fish habitat. Requirements by the latter group are particularly significant at this time as the Department of Fisheries and Oceans has recently established a policy of "no net loss or net gain" in productive capacity of fish habitats. This policy will be difficult to implement without increased understanding and development of techniques to quantify the capacity of habitats to produce fish.

This National Workshop was convened on May 6–8, 1987, at Malaspina College, Nanaimo, B.C. to review the latest techniques available to address the most important and most difficult aspect of fish habitat management: quantifying relationships between habitat features and fish production. Salmonid populations were the focus of the Workshop because of their significance in recreational and commercial fisheries on both the Atlantic and Pacific coasts of Canada. Their freshwater and estuarine habitats are located in areas where other important natural resource industries are competing for the same water supply used by salmonids and other resources in the watersheds (e.g. harvest and storage of trees, port development, and hydropower development). Further, salmonid habitats are frequently located in urban areas where the "assimilative capacity" of freshwater and estuarine ecosystems is used for the treatment of domestic and industrial wastewater. Research articles on the specific topic of the quantitative relationships between habitats and fish production are extremely scarce. The organizers therefore expanded the terms of reference of the workshop to include studies on non-salmonids which could help provide some insight into the more general problem of quantifying the effects of habitat changes on aquatic resource production.

Because Department of Fisheries and Oceans policy requires "no net loss in productive capacity of fish habitats" (Department of Fisheries and Oceans, 1986) there is now a pressing need for techniques and data to support this proactive policy quantitatively. This is particularly important because at present there is no quantitative definition of productive capacity although it appears to resemble habitat capability, in the sense used by wildlife biologists and land use planners. At any rate, development and testing of techniques to measure gains and losses of Canada's salmon habitat and resultant production will require substantial scientific effort in the immediate future. It is hoped the papers and discussions reported in these Workshop Proceedings will help guide these research efforts.

C.D. Levings
L.B. Holtby
M.A. Henderson

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Environmental Priorities: Placing Habitat in Hierarchic Perspective[1,2]

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Abstract

RYDER, R. A., AND S. R. KERR. 1989. Environmental priorities: placing habitat in hierarchic perspective, 2–12. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Habitat rehabilitation is often seen as an option open to fisheries managers for increasing yields of desirable fish species. Before rehabilitation is attempted, however, it is recommended that a broad environmental assessment be made. Emphasis is placed on the differences between the pervasive nature of environment which provides background ambience, against the localized and highly structured habitat which acts as a centre of organization and attractor for fish communities. Environmental assessment should focus first on four key survival determinants; dissolved oxygen, water temperature, subsurface light and dissolved nutrients, which constitute the principal energetic and material substances of concern. Only then, may the limiting effects of habitat be accurately determined and remedied.

Provision by managers of suitable habitat structure for the rehabilitation of fisheries is often a game of chance. Creation of artificial spawning channels to increase reproduction of stream spawning fishes may prove futile if subsequent organic sedimentation creates anoxic conditions in the interstices of the substrate, or if the real limitation to recruitment occurs later in life at some remote oceanic site.

Résumé

RYDER, R. A., AND S. R. KERR. 1989. Environmental priorities: placing habitat in hierarchic perspective, 2–12. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

La remise en état des habitats est un moyen dont peuvent souvent se servir les gestionnaires des pêches pour accroître la production des espèces recherchés. Toutefois, avant de procéder à une telle remise en état, l'on recommande de réaliser une évaluation générale de l'environnement. Les auteurs soulignent les différences entre le milieu ambiant qui constitue l'arrière-plan sur lequel se détachent les habitats proprement dits, restreints et hautement structurés, qui exercent une attraction sur les communautés de poissons et constituent leurs véritables foyers d'organisation. L'évaluation de l'environnement devrait d'abord porter sur quatre paramètres essentiels à la survie de ces organismes : oxygène dissous, température de l'eau, éclairement subsuperficielle et substances nutritives dissoutes, éléments énergétiques et substances suscitant le plus de préoccupations chez les poissons. Ce n'est qu'après avoir examiné les effets limitatifs des habitats et y rémédier.

La remise en état des zones de pêches par la reconstitution d'habitats présentant des caractéristiques appropriées est fréquemment un jeu de hasard. L'aménagement de frayères artificielles pour favoriser la reproduction des géniteurs dans les cours d'eau risque d'être inutile si, ultérieurement, la sédimentation des matière organiques crée des conditions anoxiques dans les interstices de substrat ou si les véritables facteurs qui limitent le recrutement ne surgissent que plus tard dans une zone éloignée de la mer.

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[1] Contribution No. 87-12 of the Ontario Ministry of Natural Resources, Research Section, Fisheries Branch, Box 50, Maple, Ontario, Canada.

[2] Bedford Institute of Oceanography Contribution.

A major charge typically facing fisheries managers is to increase catches of the most valued species available. Among the various options available to achieve this objective is the possibility of subsidizing or manipulating the habitat. In some instances, such as the provision of fishways to allow access to spawning habitat that is otherwise inaccessible (Clay 1961), the ensuing results can sometimes be considered obvious and unequivocal; new production occurs where it was previously impossible. In other circumstances, however, the changes in yield following a given habitat manipulation may be difficult to define with certainty in the face of normal variability of the many other, sometimes interacting, environmental factors that may affect stock production (Larkin 1974), and quantifying the effects of such changes can be at best uncertain.

In this paper, we examine some of the considerations, both theoretical and practical, that necessarily occupy managers concerned with quantifying the effects of habitat manipulations on the stocks that such measures are intended to improve. Although habitat manipulation has a long and undoubtedly useful history of application in the management of fisheries and other renewable resources, we shall show that the quantification of such effects is a difficult undertaking, unless there is prior baseline knowledge of the status of the major environmental determinants.

Our intended objective, therefore, is to stress the importance of broad environmental assessment before habitat rehabilitation is attempted. To achieve this objective we distinguish between the pervasiveness of relatively structureless environment, as opposed to the highly structured and localized nature of habitat. Our emphasis is directed at four critical environmental determinants, which should be within the zone of tolerance for target species, before proceeding with rehabilitation measures. To attempt rehabilitation measures without prior environmental assessment may not only prove to be futile, but could even be counterproductive in terms of increased abundance or yields of desired fish stocks.

Theoretical Considerations

It is platitudinous to point out that genotypes are adapted to the average conditions, and that the associated range of phenotypes must encounter and successfully cope with these. It is perhaps less obvious that the success or failure of a specific phenotype in a given milieu, is an autecological solution to an imposed set of conditions. It is individual organisms that live, thrive, or die, in the face of ambient environmental conditions. Fishery yield, or production, on the other hand, are synecological reflections of the dynamics of an ecological assemblage of diverse organisms, an expression of aggregate capacity at a level once removed from that of the individual genotypes. This is the essential nature of the problem: is it possible to argue from the autecological considerations facing the individual organism to the synecological patterns that interest the resource manager? (See comments of F.E.J. Fry, in Kerr and Lawrie 1976).

In principle, this kind of extrapolation is not reliably possible (Rosen 1978), although fisheries managers are not exempted from this task for that reason, and are regularly required to attempt the impossible. The problem is, as Fry has clearly elucidated in the fisheries context, that it is always possible to state unequivocally the probable effect of a change in a single factor such as temperature on the well-being of a target organism (Kerr and Lawrie 1976). However, it is quite another matter to attempt to do so for a species stock exposed to the many indirect and interacting pathways by which a change in environment may find expression in a natural association of organisms.

There are many examples to support this point. The fertilization experiment in Great Central Lake, Vancouver Island (Stockner 1981), for example, correctly reached the planned objective of enhanced sockeye salmon (*Oncorhynchus nerka*) smolt production, in terms of body size in particular, but did not and presumably could not have anticipated the ancillary surprises, such as the non-linear responses of the biota that were associated with increased nutrient availability (Barraclough and Robinson 1972). The theory used in the design of this experiment and the use of contagious fertilization treatments in a deep oligotrophic lake was exemplary for its time, but as experience was to show, there was a strong element of surprise in the outcome.

The world of ecosystem manipulations is full of such surprises. Generally speaking, systems theorists classify unexpected events of this kind under the general rubric of "system definition". That is, if the possible range of behaviours open to the real system does not happen to be included within the scope of the model used to plan the habitat manipulation, then surprises of this sort are not only possible, but likely. Unfortunately, although the problem of system definition is of great interest to system theorists, we know of no practical result in this area which can lead a fisheries manager to the comfortable assumption that everything that needs to be considered, has been. Ecological surprise, sometimes uncomfortably acute, will apparently be with us for some time to come (Kerr 1974; Holling 1985).

There is a second, related issue of great interest to systems theorists that is equally germane to the needs of fisheries managers. This is the question of system scale. Quite obviously, the problem of system definition can be a relatively relaxed matter at the small scales and simple biotic complexes associated with minor tributaries or small ponds and lakes. Specialists in the analysis of such systems will indubitably disagree, but the question of ecosystem complexity is very much in the mind of the beholder (Kerr 1982).

The problem of system scale becomes quite another matter at the larger spatial scales associated with major fish production systems. As spatial scale increases, so do the attendant opportunities for environmental "noise" to intrude, in the form of associated sources of environmental variability that mask the performance of the system of interest (Larkin 1974). For example, Ware (1982) concluded that it would be unlikely that the effects of hydrocarbon exploration on the fish production system of the Grand Bank of Newfoundland could be reliably distinguished from the apparently stochastic effects of other factors. By way of contrast, concerning the matter of scale, consider the different conclusions that might have been reached had a single drilling rig been conjectured to be centered in a 50 ha lake.

Habitat vs. Environment

One approach to an overview of how habitat modification might affect salmonid stocks, would be a withdrawal to a level of greater generality in order to first reiterate some fundamental ecological concepts. This approach applies particularly to those concepts which are adequately supported by baseline information. To pursue this approach further, we need to make a clear distinction between habitat, and environment or milieu. The inherent difference between these terms is often moot, unclear, or ambiguous in many ecological treatises where the individual definitions may vary from text to text (e.g. Odum 1971; Krebs 1972; Ricklefs 1973; Smith 1980). Aside from the fact that animals live in habitat, there seems to be relatively little consensus as to what attributional commonality is shared by different types of habitat. In order to clarify this issue, hopefully without provocation, we offer arbitrarily, operational definitions of habitat and environment for the purpose of our discussion.

We concur with the generic definition of Salthe (1985), that environment is a "supersystem within which a system in focus is found". This presupposes that which shall also be our premise. Our elaboration asserts that environment comprises the total physical, chemical and biological surroundings of an organism, including habitat and other biota. At this point, somewhat arbitrarily, we propose an operational definition of aquatic habitat as that component of environment which is comprised principally of physical structure including reefs and shoals, the land-water interface, zones of density stratification, whether formed from physical or chemical causes, or any other ecotone that creates a centre of organization (e.g. Francis et al. 1985). Most of the chemical and biological milieu we reserve for the more expansive definition of environment with certain exceptions, such as beds of macrophytes, which quite obviously provide a structure or break in an otherwise featureless environment, and also provide an opportunity or substrate for aggregation and biological activity.

Water, including all of its dissolved compounds, will be considered as environmental, while suspensions in the water column contributing to the level of turbidity will be accepted as habitat. The significance of these somewhat moot distinctions will unfold as we proceed with our discussion.

Essentially, the attribute of habitat that we wish to emphasize is physical structure that attracts, entrains and eventually cascades energy from one part of an ecosystem to another. By this definition, abundant and diverse habitat is a property of mature ecosystems, and forms a zone of high information content and energy potential, and low entropy (Odum 1969). Habitat serves as both an attractor and a refugium for fishes where they may feed, rest, breed and find shelter from both predators and inhospitable environmental intrusions such as high levels of subsurface illumination or strong currents. Generally, however, environment has a benign ambience, like the ubiquitous air that we breathe, and tends to be less organized and more entropic in nature than the highly structured habitat.

In addition to the arbitrary distinction made between habitat and environment, we have also approached this overview more generally, utilizing various fish species as examples. We trust that this broadening of our charge will not diminish the applicability of our conclusions to any specific taxon or its habitat, but rather, might make them more widely germane to a variety of fish-habitat interactions. Our hypothesis implies that one need not be concerned with physical, structured habitat as a limiting factor, until some of the more fundamental properties of the environment have been dealt with by hierarchic order of priority, as they are necessary for the relative well-being and survival of fishes. For this purpose, we have identified four fundamental ecosystem properties: dissolved oxygen, heat, light and nutrients, as the most critical environmental factors for fish survival and subsequent production (Fig. 1). Later we show how these four environmental determinants may be entrained through the structure of the ecosystem (habitat) to form centres of organization, or fish attractors.

Survival Determinants

The four fundamental survival determinants of the environment which we have identified (oxygen, heat, light and nutrients), do not constitute an exhaustive list of all factors critical to the survival and production of fishes, but rather are a subset of high priority. Each of these factors is entrained to differing degrees by the morphology of the system (e.g. F.E.J. Fry, in Kerr and Lawrie 1976; Fry 1984), be it the shape of a lake, including its physical habitat features, or the body form

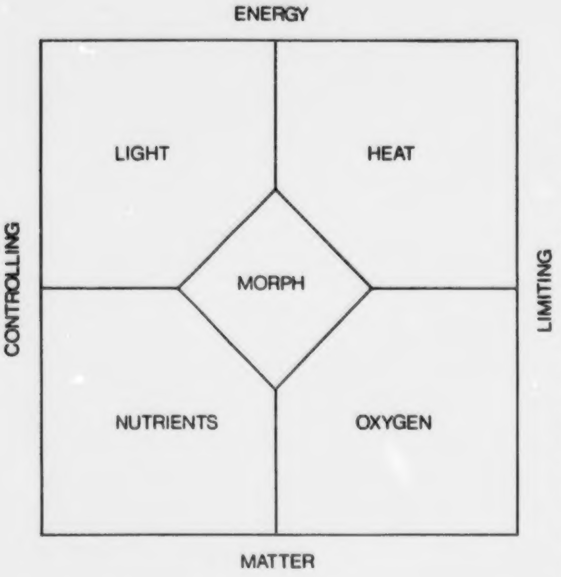

FIG. 1. Schema of four principal environmental determinants as configured and entrained by the morphology of an ecosystem, in this case, habitat. The four determinants are comprised of two energetic factors (light and heat) and two material factors (nutrients and oxygen). Light and nutrients, are controlling in the sense that they influence behaviour and/or metabolism, but are rarely lethal of themselves at any level found in nature. Heat and oxygen are controlling in their intermediate ranges, but may be limiting at the extremities, and therefore are often lethal.

of a fish or other organism. All four factors are sufficiently fundamental to be readily classified as materials or energy without a trace of ambiguity. Hence, heat and light are the principal energetic inputs affecting the survival of fishes while oxygen and nutrients constitute the two fundamental and essential material items (Fig. 1). All four factors are interrelated to varying degrees such that it is not particularly informative ecologically, to consider the effect of one survival factor on a fish in the absence of the other three critical factors. For example, temperature affects dissolved oxygen saturation levels, light controls photosynthesis, and hence, nutrient utilization and availability; photosynthesis, in turn, contributes to the concentrations of dissolved oxygen in the water column. Other interrelationships exist among the four fundamental survival determinants which may be pertinent to our discussion, but an exhaustive listing of these is not essential to our argument. Our emphasis here, is upon the need for fishes to adapt to ambient levels and ranges of each critical environmental determinant to which they are subjected, over some finite period of time, or alternatively, to utilize an appropriate avoidance behaviour when levels exceed a particular zone of tolerance (Fry 1947; Welcomme 1979).

Hierarchic Responses

The four essential environmental determinants (Fig. 1) may be classified as either energy and materials, or in another way, that is, each as either a controlling or a limiting factor (Fry 1947). All four factors may be controlling over much of their normal range in nature; that is, they are the principal determinants of behaviour and metabolic processes within a favourable milieu (Table 1). A modicum of physiological stress occurs when an environmental determinant exceeds a preferred level but remains within the zone of tolerance of a fish. When the zone of tolerance is exceeded, the determinant becomes limiting in the sense that it causes avoidance behaviour and thereby restricts Lebensraum, or when even this is precluded, results in extreme physiological stress, and ultimately, in death. Hence, light and nutrients may be considered to be controlling factors under virtually all ambient conditions found in nature, as neither is likely to become lethal under most circumstances. Dissolved oxygen and temperature on the other hand, are often directly responsible for fish mortality as in the case of winterkill (Greenbank 1945), or summerkill, when dissolved oxygen levels decrease to a level not readily tolerated by certain fish species. Dissolved oxygen and temperature sometimes interact to the detriment of some fish species during long, hot, summers, by squeezing them into a narrow pelagic zone, below which dissolved oxygen levels are too low to sustain life, and above which temperature levels are in the lethal range. Some coregonine species are adept at this environmental balancing act, the rate of survival being dependent to a large extent on the depth, volume and persistence of the tolerable zone (e.g. Fry 1937).

As a generalization, it is probably reasonable to state that survival depends on fishes satisfying their most critical needs first (dissolved oxygen, preferred temperature), at which point their behaviour becomes dependent on the controlling factors, nutrients and light. In a sense, fishes are responding to some biological variation of the Law of the Minimum (e.g. Liebig 1840) in which reaction to one environmental determinant occurs, only after reaction to other determinants of a higher priority have been satisfied. This observation was recognized by Fry (1947), who elaborated upon the mechanisms involved. He attributed the hierarchic response to the fact that limiting factors by definition, actually entered into a chain of metabolic processes of an organism. The hierarchic response to a limiting, as opposed to a controlling factor, has been aptly described in laboratory experiments such as those performed by Scherer (1971). He showed a normal response to varying levels of illumination by walleyes (*Stizostedion vitreum vitreum*), a species that is negatively phototactic at ambient daytime light intensities. However, when subjected to a respiratory stress such

TABLE 1. Means by which habitat configures and entrains four principal environmental determinants; the functional effect on the aquatic ecosystem, and the ultimate consequence to fishes.

	Environmental determinant			
	Controlling		Limiting	
	Dissolved oxygen	Temperature	Subsurface illumination	Nutrients
Habitat conformation	1) Sestonic turbidity	Density stratification	Boulder shoals; macrophyte beds	Coral reefs
	2) Gravel redds	Macrophyte beds	Inorganic turbidity	Upwelling zones
Functional effect	1) Photosynthesis inhibited; dissolved oxygen reduced	Partitions temperature	Provides shelter from light	Biological attractors
	2) Apposite levels dissolved oxygen	Reduces temperature	Occludes surface light	Entrains nutrients and energy
Consequence to fishes	1) Avoidance	Vagility constricted	Influences feeding and spawning behaviour	Aggregates fishes
	2) Successful hatch	Provides local thermal refugium	Change in diurnal movements	More efficient feeding; faster growth

as inordinately low dissolved oxygen levels accompanied by carbon dioxide accumulation, the avoidance response by walleyes to high illumination levels was temporarily discontinued (Scherer 1971). Hence, the response to subsurface illumination levels which normally regulate walleye feeding and spawning activity in a lake or stream (Ryder 1977), was abandoned in favour of a more critical and immediate concern, the need for an apposite respiratory environment conducive to survival. In lakes, fishes sometimes overcome intolerable limits of dissolved oxygen or temperature for short periods of time to make rapid feeding forays before returning to a more benign (but presumably foodless) environment (e.g. Fry 1937).

Placing priorities on single limiting factors of fishes normally subjected to several, is somewhat tenuous as there are no common grounds for comparison until death is reached. Whether low levels of dissolved oxygen or inordinately high temperatures acting in concert, place a fish's life in greater peril, is a moot point because these effects are interrelated, have different starting points, but result in the same equifinality (e.g. von Bertalanffy 1968), that is, death. There would seem to be regional discrepancies in the effects, however, that are important to evaluate before a final judgement is made on priorities of limiting factors. All things being equal, insufficient dissolved oxygen (which includes the effects of carbon dioxide accumulation), may be seen as a greater threat to a fish's life in the tropics, where rates of both organic input and putrefaction may be substantially higher than in comparable waters at high latitudes. On the other hand, tropical fishes such as *Anabas*, are often equipped with accessory respiratory organs by which they are eminently adapted to low levels of dissolved oxygen (Nikolsky 1963). Furthermore, fishes at high latitudes may have specific adaptations to low temperatures such as a complete lack of blood haemoglobin (Moyle and Cech 1982). The only reasonable and objective settlement of this dilemma would seem to come from the Law of the Minimum, which relates to only one critical factor at a time; that is, the one that most imminently threatens life.

Sorting out the relative effects of each of the two controlling factors, light and nutrients, is no simpler, as both govern species distribution, behaviour, and metabolism to differing degrees, and they are inextricably interrelated (Fry 1947). While light effects were shown to be of a generally lower priority than a deficit of dissolved oxygen and its attendant effects (Scherer 1971), their relationship to nutrient supply is less clear. What is readily apparent, however, is the higher priority placed on the two limiting factors which directly affect fish survival, as opposed to the two controlling factors, which affect mainly distribution and behaviour. Ultimately, both distribution and behaviour are as much a contributor to species survival as they are a consequence of it, but neither have an obvious or direct physiological effect that is life threatening.

Scale Effects

The four principal environmental determinants have varying and disproportionate effects, dependent upon the size and morphology of the system under consideration (Table 2). For example, dissolved oxygen is usually not of import as a limiting factor in oceans or turbulent streams. However, in lakes, it may be a limiting factor of some concern, particularly in deep, dimictic, eutrophic lakes, or in the monomolimnion of meromictic lakes such as Tanganyika (Beauchamp

TABLE 2. Influence of scale on four environmental determinants as they affect salmonids at north-temperate latitudes. The levels of effect represented are: (1) usually benign; (2) may constrain behaviour somewhat; (3) substantial behavioural and/or metabolic constraint; may be lethal if a limiting factor; (4) severe behavioural constraint; lethality common.

	Environmental determinants			
	Limiting		Controlling	
Water body	Dissolved oxygen	Temperature	Light	Nutrients
Oceans	1	1	1	1
Large lakes	2	1	2	1
Small lakes	3	3	2	2
Ponds	4	4	3	2
Large rivers	1	1	2	1
Small rivers	1	2	2	1
Streams	1	2	3	1
Brooks	1	3	3	2

1939). Similarly, ponds are extremely vulnerable to both summerkill and winterkill, due primarily to dissolved oxygen deficits (Greenbank 1945; Schneberger 1970), or occasionally, supersaturation, which is equally devastating to fish communities.

Temperature is sufficiently buffered in oceanic and large lake systems to be of relatively little concern with regard to fish survival, except in the interface zones with transoceanic currents such as the Gulf Stream, or near major upwellings (e.g. Stuart 1981). There, fishes may become entrained into water masses that have potentially lethal temperatures exceeding their individual zones of tolerance. Large, dimictic lakes have a thermal layering that often prevents effortless movements of fishes between adjacent thermal zones. However, these lakes have sufficient buffering capacity through the sheer volume of water alone, to prevent rapid temperature changes over time, except on a localized basis. On the other hand, temperature may limit fish survival in small streams or ponds at certain times of the year, because of the lack of heat buffering capacity of the small volumes of water, and correspondingly small heat budgets (Table 2).

Putting all of this in the perspective of the five species of Pacific salmon (*Oncorhynchus* spp.), it might be concluded on a general basis, that the natural oceanic environment lacks the temperature or dissolved oxygen stresses attributable to the smaller bodies of water that they might frequent during the early part of their life histories or again at spawning time. Hence the spawning streams or nursery lakes (especially in the case of the sockeye salmon) may harbour the critical limits to survival in terms of either temperature or dissolved oxygen limitations.

As an extremely rich literature exists on the limiting or controlling effects of dissolved oxygen and temperature (e.g. Fry 1947; Gibson and Fry 1954; Brett 1956; Brett and Alderdice 1958; Garside 1959; Heberger and Reynolds 1977; Shuter et al. 1980), we will dispose with further detailed elaboration of these two environmental factors.

Light — the Ecological Cleaver

Subsurface illumination, because of its environmental pervasiveness at various levels of intensity, is rarely considered to be as critical an environmental determinant as dissolved oxygen and temperature. Massive fish mortalities have never been detected due to either a surfeit or deficit of subsurface levels of illumination to the best of our knowledge. Many oceanic and lacustrine fishes such as the Atlantic herring (*Clupea harengus*), may be tolerant of ambient surface light intensities, even at high noon on a sunny day (e.g. Blaxter 1966). Other species have adapted well to a world of constant darkness as exemplified by the many cave fishes in existence (e.g. Pflieger 1975). In between these two extremes, the majority of fish species are able to tolerate the whole diurnal and seasonal ranges of subsurface illumination.

Despite these broad tolerances, the retinal response to light is not the same in all species. Some species are able to tolerate wide ranges of subsurface illumination because they possess specialized retinal structures, or have the ability to occlude light with moving pigments (Ali et al. 1977). Other species utilize the turbidity of the water column to shield sensitive retinae from the refracted sunlight of the water surface, while still others use physical structures for the same purpose (Table 1; Ryder 1977). It seems that no single retinal design is efficient at all levels of subsurface illumination over a 24 hour period. Some fishes, such as the walleye have scotopic (dim-light) vision, and are eminently well adapted to crepuscular and nocturnal feeding and spawning (Ali et al. 1977; Ryder 1977). On the other hand, a sympatric piscivorous species, the northern pike (*Esox lucius*), normally feeds and spawns only during daylight hours (Svärdson 1948; Frost 1954). Walleyes may actually be temporarily stunned at high daylight intensities, and are unlikely to be found feeding at the surface of a clearwater lake on a sunny day (Ryder 1977). Northern pike which have photopic (daylight) vision, are ineffectual feeders at night despite their extensive use of the lateral lines in feeding (Nikolsky 1963).

Accordingly, subsurface illumination may be regarded as an ecological cleaver that determines the relative dominance or subordinance of species with closely similar niche hypervolumes along the light dimension (e.g. Svärdson 1976). The effects of light may be controlled by attenuation; first, through the use of a shielding, turbid water column, and secondarily through the shelter offered by physical structure (Table 1). The availability of a turbid water column is so critical as to restrict the geographic distribution of some species, such as the sauger (*S. canadense*) and goldeye (*Hiodon alosoides*). These species thrive principally in the vestiges of the formerly large, turbid, Pleistocene Lakes of North America (Scott and Crossman 1973). There, colloidal clay suspensions result in a high turbidity that ensures a benign environment for species with scotopic vision such as the sauger, which is not as adept as the walleye at utilizing physical structure for a light shield (R.A.R. diving records). Although both of these congeneric, and often sympatric species, have modified retinae particularly suited to scotopic vision and therefore, prefer dim-light conditions, the walleye has been better adapted to moderately clear lakes than the sauger, as evidenced by its much wider distribution in North America (Scott and Crossman 1973). Ali and Anctil (1977) noted that the sauger's retina is more sensitive to subsurface illumination than that of the walleye; therefore, the sauger is best adapted to extremely turbid lakes. This conclusion was based upon: (1) the presence of more reflecting material in the sauger's tapetum and equitable distribution of it over the retinal surface; (2) a decreased abundance of single cones; (3) an increase in the rate of summation at the photoreceptor/bipolar cell integrative level; (4) and lower light intensity levels required for maximum flicker fusion frequencies (Ali and Anctil 1977).

Light, therefore, may be considered as the most important single environmental determinant for both diurnal and seasonal behaviour, as well as one of the principal factors governing the natural geographic distribution of the walleye and sauger. While both have scotopic vision, and may be expected to compete to a certain degree for a common food resource, the subtle visual differences noted by Ali and Anctil (1968; 1977) result in less subtle behaviour patterns that tend to separate these closely related species along at least one niche dimension, that of subsurface illumination. Habitat is the key exogenous feature that complements the genotype in each instance: the walleye is more broadly adapted, but shows a preference for lakes with substantial structure in the form of boulder shoals, or large macrophytes such as the *Potamogeton* species (Ryder 1977), while the sauger is most often found in lakes with uniform, heavily sedimented substrates, and with high loads of suspended matter in the water column, most usually colloidal clays (e.g. Doan 1941).

Light as an ecological cleaver between two closely related species is not unique to the walleye and sauger. Other congeneric species pairs exist that may also be ecologically separated by this single environmental determinant. Foremost among these pairs are the goldeye and the mooneye (*H. tergisus*), the white bass (*Morone chrysops*) and the yellow bass (*M. mississippiensis*), and the white and black crappies (*Pomoxis annularis* and *P. nigromaculatus*). In the case of the latter two species, when sympatric, they vary in numbers, inversely over time, as turbidity levels change. A predominantly black crappie population in Clear Lake, Iowa, changed to one constituted mostly of white crappies over a period of 8 years, closely coinciding with a gradually increasing turbidity level (Neal 1963). This author also noted that the black crappies, which preferred clear water, also utilized the physical structure and the macrophyte beds close to shore, more so than the white crappies which tended to be more pelagic, and favoured a more turbid water column. The ecological roles played by the white and black crappies, therefore, were similar to those exhibited by the sauger and walleye, respectively.

The capability of the sauger to tolerate large, structureless environments as long as the water column has an apposite degree of turbidity, makes them very adaptable to new environments created by the damming of large rivers located on old Pleistocene lake beds (e.g. Benson 1980). Hence, this species is often an opportunistic pioneer in these instances, but may later be replaced by the walleye as water levels stabilize, turbidity levels drop, and subsurface structure develops in the form of extensive beds of macrophytes (e.g. Gasaway 1970). The white crappie, however, despite its proclivity for turbid water columns, does not spawn in tributary streams in reservoirs as does the sauger, but rather requires the presence of aquatic macrophytes for spawning and nursery areas. Accordingly, white crappies may become more abundant as a reservoir stabilizes, matures, and extensive beds of macrophytes develop (e.g. Walburg 1964).

We have shown that both in nature (Ryder 1977) and in the laboratory (Scherer 1971), light is not likely to be a limiting factor of importance at the autecological level. That is, inappropriate light levels do not induce direct mortality in a species, but rather operate at the synecological level by swinging competitive advantage from one species to another. Hence, the dominant species at any given time is determined by the light regime which may swing from one optimum favouring a particular species to a different optimum favouring a second species. This subtle effect is mediated through the morph of the system, that is, the particular structure of the available habitat, be it boulder shoals, macrophyte beds or suspended matter in the water column.

Seemingly aberrant behaviour or distribution of some fish species, often attributed to inappropriate levels of dissolved oxygen or temperature (e.g. Dendy 1945; 1948), may be equally ascribed to the effects of subsurface illumination, or perhaps to a combination of effects of all three environmental determinants. Indeed, the inability of certain species to invade waters at very high latitudes may result as much from the disproportionate nature of the photoperiod there, as from the inordinately low mean temperatures.

Nutrients as an Environmental Determinant

Nutrients, as in the case of light, are rarely a lethal factor of themselves in natural systems, unless augmented to extremely high levels through cultural eutrophication (e.g. Vollenweider 1968). In these instances, the lethality is executed through another environmental determinant, dissolved oxygen, which sometimes reaches anoxic levels, even in the hypolimnions of very large lakes (Carr 1962). The hypereutrophic condition in lakes is one that is easily recognized, and its remedy (reduction of phosphorous loading), while expensive, is usually tractable (Vallentyne 1974).

Inordinately low levels of nutrients are not likely to be lethal as fish communities adapt to such situations by maintaining low levels of standing stocks through compensatory feedback. Even Waldo Lake, Oregon, sometimes said to be the most oligotrophic lake in the world, supports a modicum of fishes (Larson and Donaldson 1970).

In general, nutrients reach fishes through the intermediacy of lower trophic levels, being first absorbed by autotrophic plant life and passed up the trophic ladder through the agencies of grazing and ultimately, predation. So much has already been written about the trophic-dynamic process (e.g. Lindemann 1942) that further elaboration would be redundant, beyond pointing out the function of habitat in first concentrating, and later channeling nutrients to the upper trophic levels.

Again, the morph of the confining system is of foremost importance in channeling nutrients, be it the uniqueness of a particular habitat structure or the body form of a fish. Physical structures such as boulder shoals, macrophyte beds, and coral reefs, are known to concentrate fishes because of the food found there (Table 1). This fact has often been rapidly and opportunistically exploited by fisheries managers who enthusiastically build brush shelters, boulder shoals or tire reefs in somewhat barren aquatic habitats (e.g. Johnson and Stein 1979). These underwater structures may form centres of organization in the sense of Francis et al. (1985), which attract a variety of organisms to the newly-formed ecotone, and these in turn aggregate fishes that feed at different trophic levels. Despite the increased abundance of fishes adjacent to favourable habitat, they feed with greater efficiency (e.g. Crowder and Cooper 1979). Angling usually improves markedly in the vicinity of these structures, and locally, fishery yields may increase. Ironically, it has not been proven that total fish yield for any body of water in question increases significantly due to structural modification (Pardue and Nielson 1979). Rather, the artificial habitat tends to concentrate fishes that were already present elsewhere, through the channelization of nutrients and the subsequent attraction of plants and animals to the structure, as opposed to nutrient dissipation in the open pelagic zone.

Because of the conservative nature of aquatic ecosystems, it is unlikely in most instances, that the creation of physical structure to entrain and concentrate nutrients will effectively increase fish community production overall. Certain littoral species may, however, exhibit improved production at the expense of pelagic species occurring at the same trophic level. From a management perspective, however, this may be a desirable goal if it allows larger harvests of favoured species.

Approach to Rehabilitation

Most attempts at habitat manipulation by fisheries managers to date have been at the autecological level, with habitat erected to provide shelter, aggregate food organisms or increase reproduction rates of a target species through the provision of clean, well oxygenated spawning substrate (Table 3). Whether or not there was net beneficial gain in terms of increased yields of desired species over time seemed inconsequential as long as there was some local advantage, such as greater catch per unit of effort in a sport fishery. In extreme instances, the perceived benefit at the autecological level may actually have been a detriment to increased community yields, through a disruption of normal trophic transfer pathways. This is not to say that habitat improvement is a futile pursuit, but rather, that it should proceed from first principles, and its importance accorded the appropriate position in ecosystem hierarchy.

As an extreme case, let us consider the scenario of an aquatic system that has unduly high concentrations of an inconspicuous xenobiotic contaminant, which is threatening to the continued natural reproduction of a favoured species. Under these circumstances, the most sophisticated artificial spawning redd, technologically designed to increase levels of reproduction, will do nothing to increase either recruitment or yield. In essence, the more fundamental problem, that of water quality, must be addressed first, before any thought for the provision of artificial habitat is entertained.

A more reasonable approach to this problem would be to address habitat needs at the ecosystem level, in hierarchic perspective, and ensure that the ambience provided by the aquatic environment at least meets minimal requirements. The suitability of the ambient levels of the four fundamental environmental determinants should be considered before habitat *per se*, is assessed. It has been demonstrated repeatedly that fishes may be satisfactorily raised in essentially structureless environ-

TABLE 3. Rehabilitation measures for the minimization of ecological stresses in aquatic systems. These are accomplished by optimizing the four environmental determinants through the provision of appropriate habitat conformations.

	Environmental determinant			
	Limiting		Controlling	
	Dissolved oxygen	Temperature	Subsurface illumination	Nutrients
Habitat conformation	1) Density stratification 2) gravel redds	Beaver dams	Inorganic colloidal suspension	Macrophyte beds
Ecological stress	1) Low levels of dissolved oxygen in substrate	High water temperatures	Low levels of primary production	Excessive plant density
Proposed rehabilitation measure	1) Artificial destratification reduce sedimentation rates 2) Clean redds; construct new redds elsewhere	Remove dams; plant trees	Reduce erosion; reforestation	Reduce phosphorous loading; mechanical removal; control by herbivores

ments as long as the quality of the water meets some minimal standard (Buss et al. 1970). Fish farmers propagating fishes in silos, readily recognize this fact, and ensure that there is always sufficient water-flow to sweep away the potentially dangerous metabolites that would accumulate otherwise. Natural oceanic, pelagic ecosystems, may also be seen as essentially featureless in terms of physical organization, except for the invisible thermal bars, internal waves and subsurface currents.

A synecological approach to habitat evaluation, made initially at an ecosystem level, is advantageous in that habitat may then be perceived both in appropriate perspective and scale. Within this broader context, habitat is reduced to its elementary role — that of a centre of organization, which includes habitat as an ecotone, as a biological attractor and as a structural framework that concentrates and channels energy and nutrients where they might be most efficiently utilized by fishes. Hence, artificial spawning redds in streams may increase natural levels of Pacific salmon reproduction (e.g. the stock-recruitment relationship; Ricker 1954), but not necessarily recruitment to a high-seas fishery, as freshwater early life history is rarely the sole determinant of salmon abundance (Larkin 1979). Indeed, for the Babine Lake sockeye salmon, 90 % of natural mortality occurred during the first four months at sea and appeared to be size-related (Furnell and Brett 1986). As an inverse size-mortality relationship was observed, temperature may have been the critical environmental determinant of primary concern.

The problem is further exacerbated in that the interactive effects of the five species of Pacific salmons at the various life stages are not well known, much less of the many intraspecific stocks. This statement applies in part, to all stages of development, but probably most particularly to that of subadult and adult stages in the high seas. Consequently, construction of spawning substrate to enhance recruitment of a single species, may ultimately prove to be futile if environmental factors in the high seas tend to favour another species inordinately. In this instance, the interactive effects should first be ascertained, and the exogenous effects of the environmental determinants identified and quantified, (e.g. Svärdson 1976; Skud 1982), before any major rehabilitation initiatives are taken in terms of improving the habitat on the spawning grounds.

Conclusion

Many ecologists have previously pointed out, or at least implied, the improbability of making an alteration to one part of an ecosystem without effecting change elsewhere in the system (e.g. Holling 1985). Creating improved habitat for desirable and economically valuable species, has almost a wholesome, inoffensive, conservation connotation; however, we suggest that in most instances, the consequence at the community or ecosystem level may be unpredictable, and as often as not, undesirable from an anthropocentric point of view.

We propose that the most effective approach for the rehabilitation of a fishery, is to attempt to design with Nature (McHarg 1969) by:

1) using artificial habitat only when it is known that anthropogenic effects have reduced the extent or quality of previously existing habitat;

2) use of broad-based rehabilitation methods that solve water quality problems at the ecosystem level over a wide geographic range rather than only at a local level (i.e., reforestation of watersheds rather than the construction of rip-rap structures on eroding stream banks);

3) paying particular attention to the way single environmental variables affect species interactions by swinging dominance from one species to another (Svärdson 1976; Skud 1982);

4) approaching all problems relating to yield deficiencies or disproportionalities at the synecological and ecosystem levels first.

Acknowledgements

We are grateful to F.E.J. Fry and many of his former students who laid the foundation for much of our perspective.

We thank W.J. Christie, J. Pesendorfer, and H.A. Regier for their constructive comments on an earlier draft of this manuscript. We appreciate the many constructive comments of two anonymous reviewers of a later draft.

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Experimental Designs for Estimating Transient Responses to Habitat Alteration: Is It Practical to Control for Environmental Interactions?

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Abstract

WALTERS, C. J., J. S. COLLIE, AND T. WEBB. 1989. Experimental designs for estimating transient responses to habitat alteration: is it practical to control for environmental interactions?, p. 13–20. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Simple experimental designs involving treated and control areas, with all treatments initiated at the same time, should not be used to assess transient responses to habitat alterations. Such designs will not properly control for "time-treatment" interactions, involving differential responses for treated areas to nonrandom trends in the experimental environment. For example, survival trends for hatchery salmon stocks cannot be simply compared to survival trends in wild stocks, since the hatchery stocks may be more susceptible to changes in environmental factors such as ocean temperature. To control for such time-treatment interactions, we suggest a "staircase" experimental design in which treatment is initiated at different times on the treated units. The transient response and interaction parameters can be computed using general linear models, while correcting for temporal trends and inherent differences among units. The performance of such a staircase design is illustrated with data on the abundance of spring chinook salmon in the Salmon River basin.

Résumé

WALTERS, C. J., J. S. COLLIE, AND T. WEBB. 1989. Experimental designs for estimating transient responses to habitat alteration: is it practical to control for environmental interactions?, p. 13–20. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

De simples plans d'expérimentation englobant des zones traitées et des zones témoins, où tous les traitements sont amorcés simultanément ne devraient pas être employés pour évaluer les réactions transitoires à la dégradation des habitants. De tels plans ne permettent pas de caractériser adéquatement des interactions entre le facteur temps et les traitements, dans lesquelles interviennent des réactions différentes des zones traitées à des tendances non aléatoires dans l'environnement étudié. Par exemple, on ne peut pas simplement comparer les tendances en matière de survie des stocks de saumon d'élevage à celles des stocks naturels, car les saumons de pisciculture peuvent être plus vulnérables aux changements des paramètres environnementaux comme la température de l'océan. Pour étudier les interactions entre le facteur temps et les traitements, nous proposons un plan expérimental « en escalier », où le traitement des unités est amorcé à divers intervalles. Les paramètres relatifs aux réactions transitoires et aux interactions peuvent être mesurés au moyen de modèles linéaires généraux, en corrigeant pour tenir compte des tendances temporelles et des différences inhérentes d'une unité à l'autre. Les auteurs traitent de l'efficacité d'un tel plan « escalier » et fournissent des données sur l'abondance des saumons quinnats de printemps dans le bassin versant de la rivière Salmon.

Introduction

Political decision making and judicial action concerning fisheries habitat alteration have been relatively forgiving of uncertainty by biologists about the magnitudes of impact. In situations involving habitat damage, worst-case impacts are usually assumed; in justifying habitat enhancement, very optimistic estimates are often accepted without much critical review. The forgiving approach has been reasonable and conservative considering the difficulty, time and expense required to conduct scientifically sound field experiments that would directly measure net impacts at the population level. Such experiments are beginning to appear in the fisheries literature (e.g. Diamond 1986; Hartman 1982; Murphy et al. 1986), and they have provided a variety of "surprising" results compared to predictions based on laboratory data on fish behavior and physiology. For example, there may be a net increase in coho salmon production from logged watersheds, in spite of obvious deleterious effects associated with siltation (Hartman 1982). As such results become available, and as other pressures on water resources grow, we can expect political and judicial decision making to become much more critical and demanding; we are going to have to provide clearer field evidence of net impacts, and to show that the evidence cannot be explained by "extraneous" factors such as environmental trends and cycles such as El Nino events.

This paper discusses the general problem of estimating transient responses to habitat change in field situations where there may be progressive, cyclic, or irregular impacts also occurring due to uncontrolled factors such as climate change or progressive development of distant fisheries. By a transient response we mean any pattern of population size or population rate change over time that does not involve just a sudden shift from one level to another. For example, habitat improvements may cause an immediate increase in abundance, followed by a progressive decline back to pretreatment levels as various ecological changes occur in response to the improvement.

The following section reviews alternative approaches to impact measurement (pre- vs. post-treatment comparisons, planned experiments, etc.), highlighting criticisms that might be levelled at the scientific validity of the simpler approaches. The next section introduces an experimental design we call the "staircase" (Walters et al. 1988) that avoids three key weaknesses of simpler designs (local uniqueness of behavior, confusion of responses with effects of environmental trends, and differences between treated and control areas in response to environmental trends). Next, we discuss general design trade-offs related to the duration of pre- versus post-treatment monitoring, the number of control units, etc. for an experiment of fixed size. Finally, we deal with the question of choosing an efficient and effective set of experimental units (areas, steams, etc.) to use in a staircase design; this choice is critical in determing how large (and costly) the design needs to be, and may preclude entirely the development of a fully defensible design. Further analyses and statistical details on the staircase design may be found in Walters et al. (1988); our purpose here is to provide a review for readers who are concerned with the logic and interpretation, but not the quantitative details, of experimental design for measuring transient responses in variable environments.

Approaches to Impact Measurement

Simpler approaches to impact measurement and design of field experiments have been well reviewed by Green (1979), Hurlburt (1984), Millard and Lettenmaier (1986), and Stewart-Oaten et al. (1986). When looking at a particular case situation, the impact measurement question can be stated as: "How does the behavior of this treated system differ from what it would have been in the absence of treatment?" Phrased this way, it is clear that there is no scientific way to guarantee answering the question correctly because there is no way in nature to both treat and not treat the same case systems, at the same time.

Given that there is no scientific way to be sure of correctly measuring the impact, it is necessary to rephrase the impact measurement question into a more modest one that can be approached empirically. Three heuristic rephrasings that have been widely used are:

1. Is the post-treatment behavior unlikely in view of past experience with the system?
2. Is the behavior unlikely in view of how other, similar ("control") systems have behaved since the treatment?
3. Is the new behavior repeatable (reproducable) when other (replicate) systems are subject to the same treatment?

Each of these questions involves making some prediction about how the initial case system would have behaved had it not been treated; that is, each involves some way of modelling that unobservable behavior.

The first heristic question leads to the idea of making pre- versus post-treatment comparisons on the same experimental unit. In essence, the pretreatment data are used to construct a model to predict a baseline against which to compare the post-treatment behavior. There is no way to avoid having such a model, even if it is very simple (e.g. mean of past data), and one need not be a strong critic of modelling to identify a host of ways that such a model can (and very probably will) fail. Even in situations where very long baseline time series of population data are available, we end up seeing several alternative and equally plausible explanations for each major change that has occurred. For example, in the Great Lakes there is still debate about the relative importance of fishing, habitat change, and lamprey mortality in causing declines of lake trout. In British Columbia there is debate about whether declines in survival rates of hatchery salmon have been due to factors operating in and around the hatcheries (disease, genetics, etc.) or to changes in the marine climate (temperature, upwelling, etc.); there are quite credible models and detailed data to back up both possibilities. There appears to be a growing scientific concensus that pre-versus post-treatment comparisons are simply too risky and misleading a way to study population responses.

Questions two and three lead to the classic concepts of replication and control in experimental design. It is reasonable to hope (but by no means scientifically guaranteed) that several units (streams, areas) within a region will respond similarly to some of the uncontrolled changes that would haunt a pre- versus post-treatment comparison, since these units will be subject directly to at least some of the same factors (large-scale climate changes etc.). This hope can be replaced with stronger, probabilistic statements of confidence where it is feasible to monitor several replicate treated and control units, and to deliberately randomize the choice of which units will be treated. An important point here is to heed the warnings of Hurlburt (1984) about "pseudoreplication": adding more measurements per unit (more times, sampling stations in each unit, etc.) is of strictly limited value; the critical need is to monitor additional, independent units.

The third question does not lead directly to practical heuristics for environmental and resource management research. It may be true in the very long run that we will understand precisely how logging influences salmon only by seeing how very many salmon streams respond to logging, at different times (e.g. different ocean conditions) and places. However, another question is raised that may be practical and important to answer in the short term: do apparent responses to treatment depend strongly on when the treatment is applied, or, in statistical parlance, is there a strong "time-treatment" interaction? We might expect, for example, that logging would have less influence on a salmon population during a time of good conditions for ocean survival than during a time when conditions permit only the healthiest smolts to survive.

Time-treatment interactions are critical for resource management decision making, since the very possibility of an interaction being present can provide an apology for continuing bad management policies. For example, declines in chinook and coho hatchery survivals have been blamed on oceanographic factors that may reverse themselves if we are patient and let the hatcheries keep going. When data are presented showing that survival rates of wild stocks have not experienced the same decline, the rejoiner is simply that hatchery fish are more vulnerable to oceanographic changes than are wild fish (i.e. wild fish are not a valid control because hatchery survival depends on time differently than wild survival). Unless an experimental design somehow allows for measurement of the time-treatment interaction effects, it will inevitably leave resource managers with excuses to do whatever they want, always blaming any failures on uncontrolled outside agents or factors. The next section discusses one experimental design, the staircase, that does provide a way to estimate the interaction effects.

The Staircase Design Model

The previous section noted three key sources of uncertainty in the interpretation of data from simple experimental designs such as pre- versus post-treatment comparisons: (1) local uniqueness in temporal behavior of treated units (i.e., any unit may have a unique trend not reflected by other, so-called control units), (2) temporal behaviors due to factors such as climate that are shared by all experimental units, and (3) time-treatment interaction (i.e., treated units may respond differently to factors such as climate change than do untreated units). A simple experimental design model representing these sources of variation is:

$$(1) \qquad Y(i,t) = U(i) + T(t) + R(t\text{-}t_i) + I(t\text{-}t_i,t) + e(i,t)$$

where $Y(i,t)$ is the measured response in experimental unit i at time t, $U(i)$ is the (locally unique) mean response of unit i over all times, $T(t)$ is a time effect shared by all units at time t, $R(t\text{-}t_i)$ is the mean response of a unit for which treatment began $t\text{-}t_i$ times ago ($R=0$ for $t\text{-}t_i<0$), $I(t\text{-}t_i,t)$ is the interaction effect at time t for units treated $t\text{-}t_i$ times ago (present only in treated units, unlike $T(t)$ which is present for all units i), and $e(i,t)$ is the locally unique response (including measurement errors) of unit i at time t.

Here we envision that the $U(i)$ and $e(i,t)$ can be forced to be random effects by deliberate randomization in the selection of experimental units i from some large universe, and by randomization in the assignment of units to treatments. However, there is no pretense that the $T(t)$ and $I(t\text{-}t_i,t)$ are random variables; they may assume any complex pattern over time t, such as trends, cycles, or abrupt shifts at particular times. It would be a pseudoreplication error (sensu Hurlburt 1984) to pretend that the $T(t)$ are random. Note that the $e(i,t)$ may not be random over time since there may be unique local trends; all that we can do by randomization is to insure that on average the $e(i,t)$ over i for any t and over t for any i will not systematically mask the treatment effects R and I.

If it were not for the $I(t\text{-}t_i,t)$ interaction effects, it would be obvious how to design an experiment to estimate the U, T, and R effects in the design model of Eq. (1). Taking several units (so as to average across any locally unique effects $e(i,t)$), observe all units for some pretreatment times so as to estimate the $U(i)$. Then treat a subset (for a blanced design, about half the units) leaving the others as controls to measure the $T(t)$ effects. Finally, compare the treated and untreated units to estimate the $R(t\text{-}t_i)$. Essentially this design has been recommended by Green (1979) and Stewart-Oaten et al. (1986).

However, if treatment is initiated on all treated units at the same time, t_i, it is logically impossible to distinguish between the $R(t\text{-}t_i)$ and $I(t\text{-}t_i,t)$ effects of Eq. (1). In other words, it is impossible to tell whether the measured responses are "typical" of time since treatment (t-t_i) independently of the particular time, t, or are instead just due to environmental interaction effects $I(t$-$t_i,t)$ associated with the particular times when the experiment is conducted.

The basic concept of the staircase design (Fig. 1) is simply to initiate treatment at more than one starting time, t_i. This leads to a staircase appearance in a diagram showing which units are treated at different times. Given at least two treatment starting times, it is logically possible to contrast the $R(1)$, $R(2)$, etc. effects observed at different times with the $I(t)$ effects seen at those times so as to distinguish among most of the effects (In the linear algebra of solving for the R's and I's, a few particular effects remain confounded; see Walters et al. 1988 for details.). If it is further admitted that the I effects may depend on the time since treatment, t-t_i, as well as the time, t, then it is necessary to keep adding new treatment units over time (e.g. to see the $I(1,t)$ effects, one must keep providing new observations of the response $R(1)$ at the first time after treatment.). Also, it is in principle necessary to replicate the initiation of treatment at each starting time. Thus while the staircase design illustrated in Fig. 1 appears quite simple, the treatment sequence needed to really distinguish among all possible effects will necessarily be quite complex and will involve treating many experimental units.

If pretreatment data indicate that all experimental units have purely random variations, $e(i,t)$, after accounting for the shared time effects, $T(t)$, then the absolute minimum sized staircase design can be used; this design must have at least three experimental units: one untreated control, one unit treated after at least 1 year of untreated observation, and one unit treated in the very next time step. If the second treatment unit is started after more than one time step, every other I effect will be confounded with the R effects. It must be further assumed under this minimum design that the interaction effects (I) depend only on time and not on the time since treatment. That is, one must assume that treated units respond the same to each environmental event no matter how long it has been since they were treated.

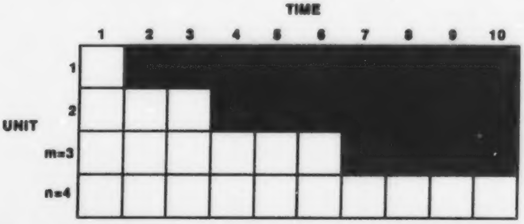

FIG. 1. In this basic "staircase" design, shading indicates treated time-unit combinations. Interaction effects that are independent of time since treatment can be estimated when more than three experimental units are used provided treatment starts in successive times or else at uneven times as in this example where $t_1=1$, $t_2=3$, $t_3=6$, $n=4$, $D=10$.

As an example of the distinction between the staircase and simpler experimental designs. consider the current situation in British Columbia with hatchery chinook and coho salmon production. It was noted earlier that survival declines have been attributed by some to oceanographic factors; an altenative hypothesis would be that conditions for survival decline progressively in the presence of high rearing densities (due to disease, predators, etc.). Suppose the Canadian government suddenly decided to accept this alternative, and to insist on lowered rearing densities in all production facilities. This "experimental" policy change would provide only pre- versus post-treatment control; any response (or lack of response) seen in all the facilities could equally well be due to the policy change or to further oceanographic change that happened to coincide with the time of policy change. An improved experiment would be to reduce rearing densities in only a subset of the facilities; this would permit measuring the initial response to reduced density (relative to high density "control" facilities), but could be misleading if the response develops over an extended time as a transient pattern. To insure that the response pattern is in fact general (not just due to interaction between reduced density and the ocean conditions prevalent during the first density reduction), it would be necessary to initiate reduced density treatment of another subset of facilities at a later time; the overall design would then have the staircase structure.

It is important to notice that the staircase design structure makes no particular assumptions about the "shape" of the transient response curve over time (values of R versus t-t_i) or of the curves of $T(t)$ and $I(t)$ over time. Apparently simpler and more efficient designs might be obtained by assuming particular shapes or functions for these curves, but at the risk of obtaining misleading results if the assumed shape turns out to be incorrect.

Design Configurations Given a Fixed Experiment Size

Given that a staircase design is considered necessary and that it must satisfy the minimal criteria noted above, what is the expected performance of various design alternatives? In an experiment of fixed duration (D) and number of units (n) there are three trade-offs to consider: the number of treatments started each year, the initial pretreatment time (t_1), and the number of control units (n-m). The performance of alternative designs can be evaluated by the expected variance of the response parameters, $R(k)$ (Walters et al. 1988), the goal being to minimize these variances. Note that for an experiment of fixed size, the error variance (s^2) can be ignored since it will be the same in all comparisons of the parameter variances.

The first trade-off is whether to spread out or to clump the treatment starting times (t_i). If one is primarily concerned with estimating the mean transient response, it is best to spread the treatment starting times over as many times following t_1 as possible. On the other hand, if one is more concerned with the initial response, $R(1)$, it is best to start all treatments at times t_1+1 and t_1+2 (Walters et al. 1988, table 1). If there are more treatment units than treatment times ($m>T-t_1$), the "excess" units can be used to replicate treatments. An obvious choice is to replicate the earliest treatments so as to improve estimation of the year-one response, $R(1)$.

The second trade-off is a short versus long time before the first treatment is started (t_1). A longer pretreatment time allows the mean responses of each unit, $U(i)$ to be more accurately estimated, and consequently to be better distinguished from the transient responses, $R(k)$. On the other hand, a long pretreatment time limits the number of treatment starting times (t_1) and the duration of the transient response (K) that can be estimated. Within these limits, the variance of the response parameters decreases with increasing pretreatment time, but this improvement is modest (Walters et al. 1988, table 2).

The third trade-off is the number of treatment units (m) versus control units (n-m). More control units allow the time effects, $T(t)$, to be more accurately distinguished, but limit the number of observations of each response parameter, $R(k)$. In general, the optimal number of control units is roughly equal to $n/4$ (Walters et al. 1988, table 3). This is fortunate from a management viewpoint because it calls for monitoring relatively few untreated units; such monitoring is often politically difficult to justify.

Effect of Experiment Size on Design Performance

This section addresses the question of how big an experiment need be to estimate the parameters of a transient response, and how the experimental units should

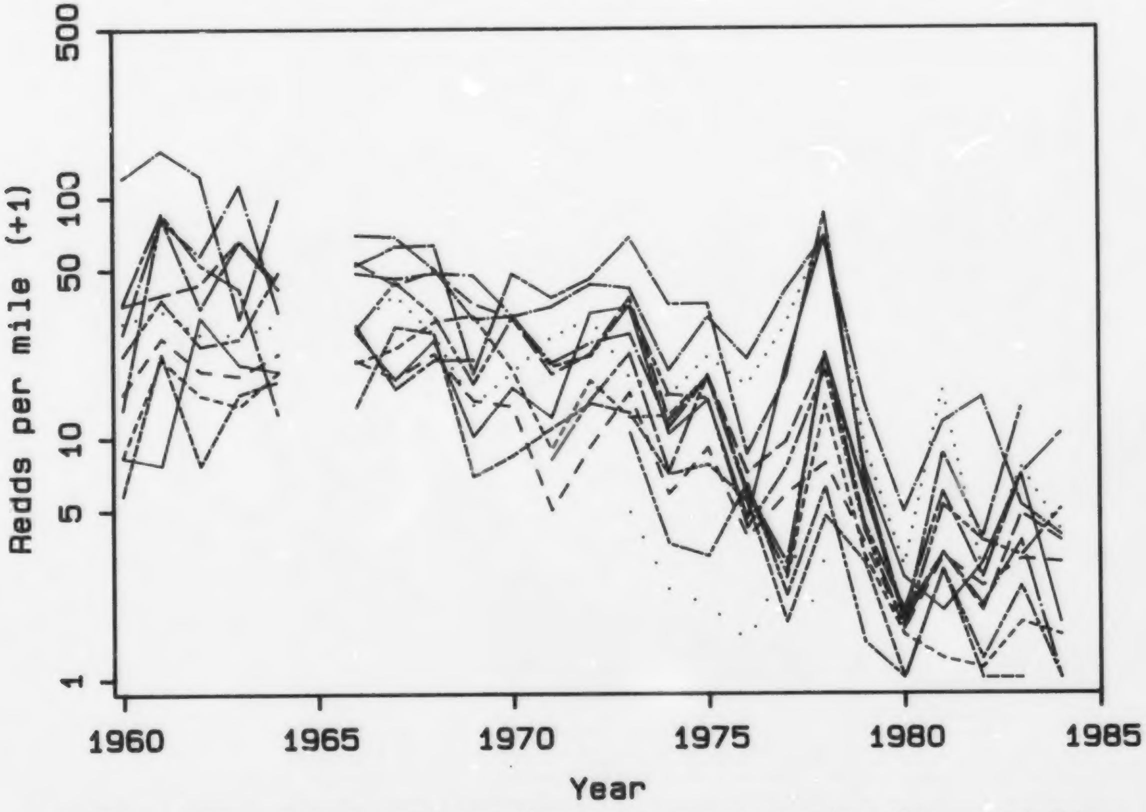

FIG. 2. Relative abundance of spring chinook salmon (*Oncorhynchus tshawytscha*) spawning in 13 streams in the Salmon River basin (a tributary of the Snake River). The redd counts were incremented by one to permit plotting on a log scale. There was no survey in 1965. The data are from Schwartzberg and Roger (1986).

be selected. On one hand, it is important to include as many units as possible in order to avoid confounding the response parameters, $R(k)$, with non-random patterns in the residuals, $e(i, t)$, of treated units. If the set of experimental units (n) is chosen randomly from the universe of potential units, the error variance (s^2) should be independent of n.

The field ecologist, however, does not have the luxury of creating identical experimental units. In nature there is not an unlimited supply of similar replicates; larger experiments will have to include an increasingly diverse set of units. In many situations it may be preferable to deliberately choose a subset of similar experimental units, provided that this subset adequately represents the remaining units. Similarity of experimental units can be measured by standard cluster analysis of historical data on each unit over time.

For example, we analyzed data on the abundance of spring chinook salmon (*Oncorhynchus tshawytscha*) spawning in 13 streams in the Salmon River basin from 1960 to 1984 (Fig. 2). The abundance index is the number of redds counted per mile of stream surveyed. The main feature of Fig. 2 is a downward trend in abundance during the 1970's, but considerable among-stream variability is apparent. After removing the stream means, $U(i)$, and time trends, $T(t)$, by two-way ANOVA, we clustered the streams according to similarity of the residuals, $e(i, t)$, over time (Fig. 3). Geographic patterns are evident in the cluster diagram: the five streams on the middle fork all cluster together; three of the tributaries of the main branch cluster together, but two others are quite dissimilar.

If experimental units are ranked according to similarity, error variance (s^2) is a increasing function of

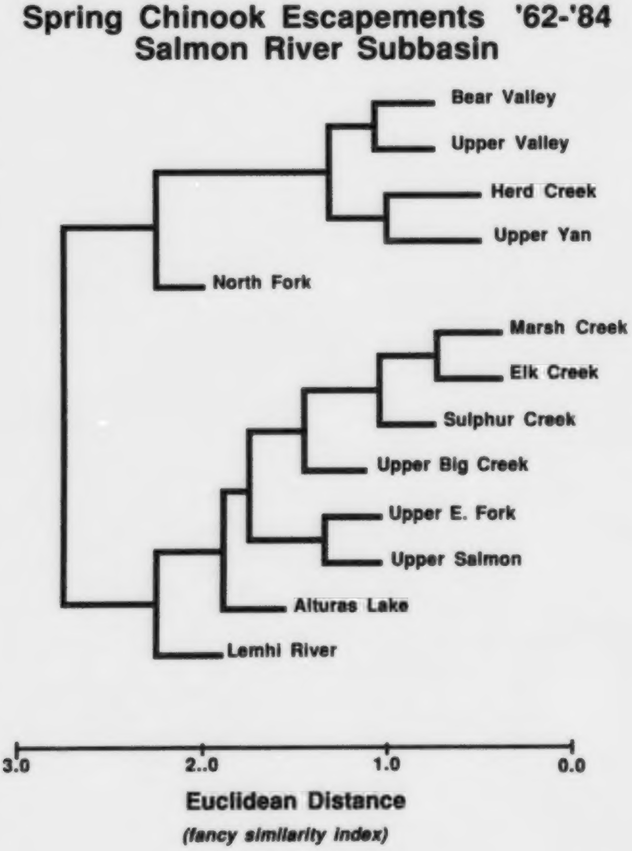

FIG. 3. Similarity in abundance of spring chinook spawning in 13 streams in the Salmon River basin. Group average sorting was used to cluster the residuals, $e(i,t)$, remaining after the redd counts were log transformed, and the stream means, $U(i)$, and time trends, $T(t)$, were removed. A smaller Euclidean distance means that the streams are more similar over time.

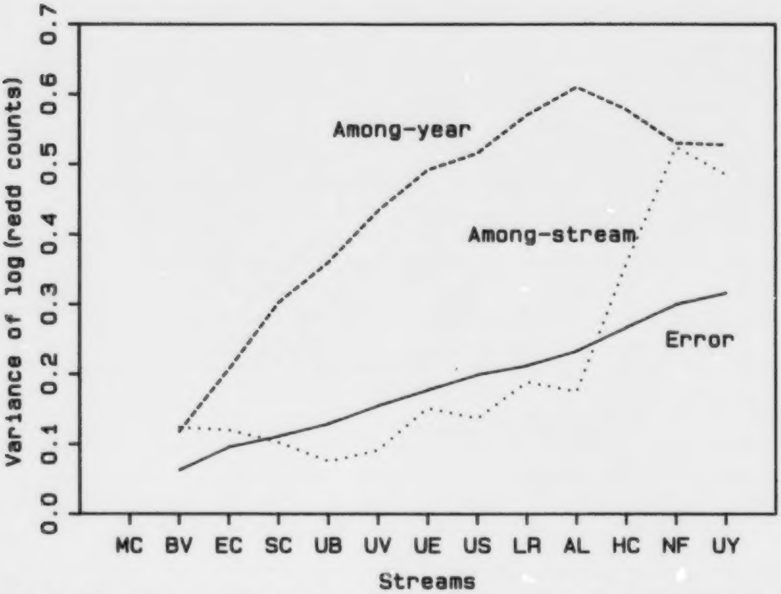

FIG. 4. Variance of log(redd counts) as a function of the number of Salmon River tributaries included in the experimental design. Solid line — error variance; dotted line — among-stream variance; dashed line — among-year variance. The streams were ranked according to the cluster analysis and the initials, refer to individual streams: MC — Marsh Creek, BV — Bear Valley Creek, EC — Elk Creek, SC — Sulpher Creek, UB — Upper Big Creek, UV — Upper Valley Creek, UE — Upper East Fork, US — Upper Salmon River, LR — Lemhi River, AL — Alturas Lake Creek, HC — Herd Creek, NF — North Fork, UY — Upper Yankee Fork.

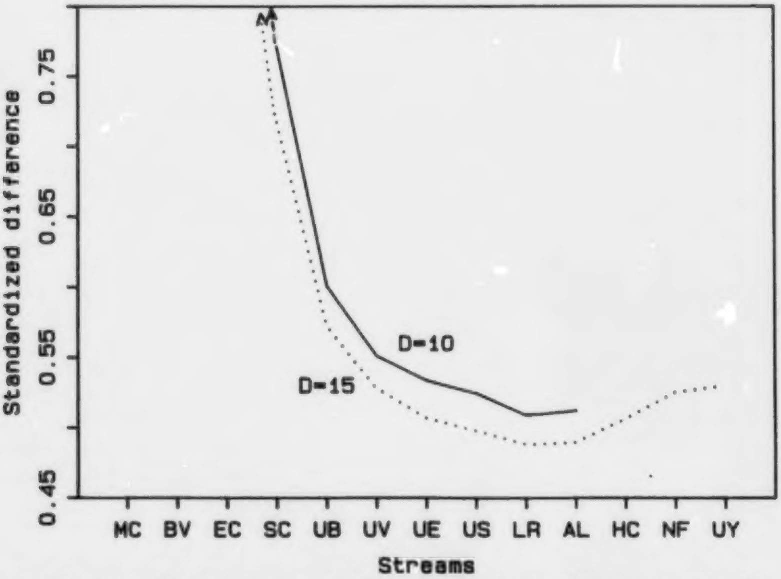

FIG. 5. Minimum statistically significant response in the third year of treatment, $R(3)$, as a function of the number of streams included in the experiment. The detectable diference was calculated as the product of estimated parameter standard deviation times error standard deviation (Fig. 4) times the t statistic at the 0.05 level with $\mathrm{df}=n(D-1)-3D+2t_1+2$. This difference (in log units) was standardized by dividing it by the grand mean redd count (2.6). The staircase design has one control creek ($n-m=1$), pretreatment time is one ($t_1=1$), and a new treatment is initiated each year provided a sufficient number of streams and/or years. Solid line is for an experiment of 10 years duration, dashed line, 15-year duration. Initials are the same as in Fig. 4.

experiment size (*n*) perhaps with jumps as new clusters enter the set. For the Salmon River basin streams, error variance increases almost linearly with the number of streams added, while the variance explained by shared time effects increases initally and then levels off (Fig. 4). The variance explained by stream means increases slowly as streams of the same size are added and then increases sharply as the final small streams are added. Variance is greatest for an intermediate number of streams. There may be an optimal experiment size (5 to 10 units) which balances the benefit of more units in decreasing parameter variance against the penalty of increased error variance (Fig. 5). Beyond this size, it may be necessary to repeat the basic staircase design on another block as identified by cluster analysis. In the Salmon River basin, an obvious choice would be to perform the basic staircase design on the five Middle Fork streams and to repeat this design on the five Main Branch tributaries.

The choice of experimental duration (*D*) is not as critical as the number of experimental units. Obviously, the minimum duration is the pretreatment time (t_1) plus the duration of the response (*K*). Beyond this, the manager can use an adaptive decision rule to decide when to terminate the experiment. For example, the experiment could be terminated when the response parameters, $R(k)$, have been estimated to a desired accuracy. Note that a longer experiment duration does little to improve the estimates of initial responses (e.g. $R(3)$ in Fig. 5) unless new treatments continue to be added.

Conclusions

To fully provide for replication and randomization, and to properly control for time-treatment interaction, a staircase experimental design should involve at least six experimental units (streams, watersheds, etc). On the other hand, it may be difficult in most field situations to even find six units that are reasonably similar in structure and historical behavior, and it may be prohibitively expensive to monitor so many units over a sufficiently long study period (pretreatment plus transient times). Also at least two of the six units should remain untreated over the whole study period, thus involving an economic cost of foregone development opportunities.

On balance, it appears that scientifically defensible, well designed experiments will often not be justifiable for estimating the effects of large-scale habitat changes in the field. Where good experiments cannot be justified, the key question should be which of several bad assumptions to make in defining an acceptable design. A minimum staircase design (with three experimental units) is one possibility, where it would have to be assumed that there are no locally unique population trends (or other more complex behaviors) not shared among the units. Compromise to less than three experimental units makes it impossible even in principle to distinguish transient treatment effects from environmental effects, so when less than three units are feasible we may just as well stay with only one and just make (foolish) pre- versus post-treatment comparisons.

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Utility of Spawner-Recruit Relations for Evaluating the Effect of Degraded Environment on the Abundance of Chinook Salmon, *Oncorhynchus tshawytscha*

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Abstract

REISENBICHLER, R. R. 1989. Utility of spawner-recruit relations for evaluating the effect of degraded environment on the abundance of chinook salmon, *Oncorhynchus tshawytscha*, p. 21-32. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Spawner–recruit relations provide a valuable conceptual framework for predicting the effects of habitat alteration on the productivity and abundance of anadromous salmonid populations. These effects should result in shifts in the spawner–recruit relations; however, actually detecting such shifts has proven difficult. I used simulation modeling to investigate the effects of environmental variability, and of errors present in spawner–recruit data sets, on the bias and precision of estimates of spawner–recruit relations and on the sensitivity for detecting shifts in these relations. The simulations, which were patterned after an analysis for chinook salmon (*Oncorhynchus tshawytscha*) in California, showed that spawner–recruit relations are generally estimated with low precision (often with bias) and that less than twofold shifts in productivity or carrying capacity are unlikely to be detected. In addition to accurately estimating the numbers of spawners, the age and sex composition of spawners, and the harvest, one must account for density-independent variation in survival if spawner–recruit analysis is to be a sensitive tool for detecting and measuring the effect of environmental degradation.

Résumé

REISENBICHLER, R. R. 1989. Utility of spawner-recruit relations for evaluating the effect of degraded environment on the abundance of chinook salmon, *Oncorhynchus tshawytscha*, p. 21-32. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Les relations géniteurs–recrues fournissent un bon cadre théorique pour prévoir les effets de la dégradation des habitats sur la productivité et l'abondance des populations de salmonidés anadromes. Ces effets devraient entraîner des modifications à l'égard des relations géniteurs–recrues; mais il est en fait difficile de déceler de telles modifications. J'ai utilisé des modèles de simulation pour étudier les effets de la variabilité des caractéristiques de l'environnement et des erreurs dans les séries de données concernant les rapports géniteurs–recrues sur le biais et la précision des estimations des relations géniteurs–recrues et la capacité du modèle de déceler des modifications dans ces relations. Les simulations, dont les tendances s'inspirent d'une analyse des saumons quinnats (*Oncorhynchus tshawytscha*) réalisée en Californie, ont révélé que les estimations des relations géniteurs–recrues sont généralement peu précises (et comportent souvent un biais), et qu'il est peu probable de pouvoir déceler des différences correspondant à moins du double de la productivité ou de la capacité biotique. En plus d'estimer avec exactitude le nombre de géniteurs, la composition âge-sexe de ces derniers et les captures, il faut tenir compte des variations du taux de survie qui ne sont pas liées à la densité afin que le modèle des relations géniteurs–recrues soit suffisamment sensible pour déceler et mesurer les effets de la dégradation de l'environnement.

Introduction

Spawner–recruit relations provide a valuable conceptual framework for predicting the effects of habitat changes (Junge 1970; Cederholm et al. 1981) or genetic alterations (Reisenbichler and McIntyre 1977) on the productivity and abundance of anadromous salmonid populations; such effects are reflected by shifts in the spawner–recruit relation (Fig. 1). Spawner–recruit relations are valuable for evaluating such changes because they show the net effect over the entire life cycle and across a broad range of fish densities, e.g.

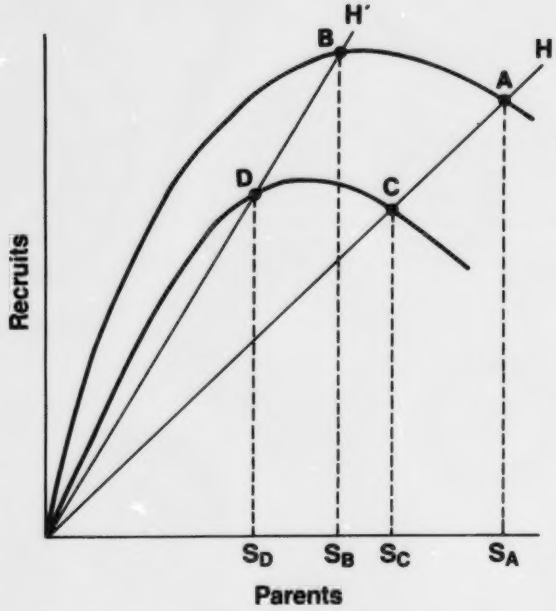

FIG. 1. Hypothetical spawner–recruit relations for a salmon population. Degraded environment causes the relation to change from the upper curve to the lower curve, whereas increasing harvest from *H* to *H'* simply moves the equilibrium point from *A* to *B* on the upper curve, or from *C* to *D* on the lower curve. S_A, S_B, S_C and S_D are the equilibrium numbers of spawners associated with points *A–D*.

spawner–recruit relations can be used to consider habitat alteration, fishing, and density-dependent mortality simultaneously. Consequently, knowledge of spawner–recruit relations can lead to better predictions of the effects of environmental changes, better adjustments of harvest to accomodate these changes, and better understanding of the biology of the fish than is possible without consideration of density-dependent responses of populations.

Density-dependent reproduction, growth, and mortality determine the shape of spawner–recruit relations, while variation in environmental conditions causes the points to be scattered about the relation. Although spawner–recruit relations are extremely valuable for conceptualizing the effects of changes in environment or in fishing, their precision for actually measuring environmental change or managing fisheries is limited by environmental variation (Gulland 1974; Pella and Myren 1974).

When environmental variation does not preclude the estimation of spawner–recruit relations, accurate estimates of the numbers of spawners (escapement) and of the associated numbers of recruits (recruitment) are required for reliable results. For populations severely reduced by fishing, inaccurate estimates of escapement mask the true spawner–recruit relation so that the maximum productivity (recruits per spawner at the origin) is typically overestimated and the population sizes for maximum sustained yield or maximum recruitment are underestimated (Walters and Ludwig 1981).

Despite problems with environmental variation and the quality of data, spawner–recruit relations have been developed and shifts in these relations have been reported for sockeye salmon (*Oncorhynchus nerka*) and chinook salmon (*O. tshawytscha*). Shifts were noted for sockeye salmon in the Chignik Lakes, Alaska (Dahlberg 1973); the Columbia River (Junge and Oakley 1966); Karluk Lake, Alaska (Rounsefell 1958; Tanaka 1962; Van Cleve and Bevan 1973); and the Skeena River, British Columbia (Tanaka 1962). Shifts were noted for chinook salmon in the Columbia River system above Bonneville Dam (Junge and Oakley 1966; Van Hyning 1973; Salo and Stober 1977; Horner and Bjornn 1980a, 1980b; Irving and Bjornn 1980); in the Rogue River, Oregon (J.A. Lichatowich, Oregon Department of Fish and Wildlife [ODFW], 303 Extension Hall, Oregon State University, Corvallis, OR 97331, unpublished data); in the Umpqua River, Oregon (A. M. McGie, ODFW, 303 Extension Hall, Oregon State University, Corvallis, OR 97331, unpublished manuscript); and in the Sacramento, San Joaquin, Shasta, and South Fork Eel rivers, California (Reisenbichler 1986). Although these analyses suggested that habitat change can be evaluated from spawner–recruit analyses, the accuracy and statistical sensitivity of the analyses was unknown.

The purpose of the present work was to investigate, with simulation modeling, the effects of environmental variability, and of measurement errors present in spawner–recruit data sets, on the bias and precision of estimated spawner–recruit relations and on the sensitivity for detecting shifts in these relations. The effects of three sources of error were evaluated: (1) lack of annual age and sex composition data (i.e. numbers of recruits estimated from simplified age compositions, and male spawners not distinguished from female spawners); (2) errors in the estimated numbers of spawners; and (3) errors in the estimated values for harvest fraction.

The simulations were patterned after Reisenbichler's (1986) analysis for chinook salmon in California, the only analysis to test spawner–recruit relations for significant shifts resulting from specific habitat alterations (water development projects). He found an approximately 50 % reduction in productivity (e.g. recruits per spawner at the origin, at maximum sustained yield, and at maximum recruitment) associated with the first bankfull flood after completion of Shasta Dam on the upper Sacramento River (presumably resulting from loss of gravel below the dam); an approximately 50 % reduction in carrying capacity associated with the operation of a low-head (6-m) irrigation diversion dam on the upper Sacramento River; and an approximately 75 % reduction in productivity associated with massive withdrawals of water from the lower San Joaquin River during the period of smolt emigration. Unanticipated shifts of similar magnitude were detected in two other streams. The spawner–recruit data were developed from estimated numbers of spawners (without annual estimates of age or sex composition, except that age 2 spawners [grilse] sometimes were estimated separately from older spawners) and estimated harvest fractions, and were fitted to the model of Ricker (1954) by simple linear regression of log-transformed data (Ricker 1975).

Materials and Methods

A model developed to mimic a population of chinook salmon reproducing according to the Ricker spawner–recruit model, yielded "observations" of the escapement for a specified number of years. The model was based on the following conditions:

(1) $R = \alpha' \mathrm{F} e^{(-\beta' F + v)}$, where R is the number of progeny surviving to age 2, F is the number of female spawners, v is a normally distributed random variable with mean 0.0 and variance s_v^2, and α' and β' are the parameters for the Ricker model, adjusted for female spawners only;
(2) males and females occur in equal proportions among age 2 progeny;
(3) all fish mature as 2-, 3-, or 4-year-olds, with only males maturing at age 2;
(4) only fish older than age 2 are taken by the fisheries;
(5) all natural mortality occurs before fish reach age 2, i.e. before fish enter the fishery;
(6) no noncatch fishing mortality;
(7) each year all harvest (of both immature fish and maturing fish) occurs before mature fish enter fresh water so that the probability of being caught during the third year of life is the same for fish that would mature at age 3 as for fish that would mature at age 4; and
(8) the expected number of offspring is the same for age 3 and age 4 females.

For convenience, some of these conditions are more restrictive than those used by Hankin and Healey (1986) in a similar age-structured model, e.g. Hankin and Healey included natural mortality occuring after fish entered the fishery, and age-specific fecundities. The effect of such differences should have been negligible for the purposes of this work.

The variables or parameters used in the simulation are summarized here for reference; they are introduced elsewhere in the text as the model is further described.

R_i	Number of progeny from the *i*'th year-class surviving to age 2.
B_{ij}	Number of *j*-year-old males from the *i*'th year-class that survive to spawn (in year $i + j$).
G_{ij}	Number of *j*-year-old females from the *i*'th year-class that survive to spawn (in year $i + j$).
M_i	Number of male spawners in year *i*.
F_i	Number of female spawners in year *i*.
T_i	Total number of spawners (male and female) in year *i*.
E_i	Estimated number of spawners in year *i*.
H	Harvest fraction.
h_i	Annual harvest rate for year *i*. Normally distributed random variable with mean h and variance s_h^2.
p_{ij}	Proportion of spawners in year *i* that are *j* years old.
w_i	Proportion of spawners in year *i* that are female.
m_{ij}	Proportion of 2-year-old males of the *i*'th year-class that would mature at age *j*.
f_{ij}	Proportion of 2-year-old females of the *i*'th year-class that would mature at age *j*.
v	Multiplicative environmental factor included in the spawner–recruit relation $R_i = \alpha F_i e^{(-\beta F i)} e^v$. Normally distributed random variable with mean 0.0, and variance s_v^2. Values for s_v^2 were 0.10, 0.20, and 0.50.
u	Multiplicative (escapement) error factor used to obtain E_i from T_i: $E_i = T_i e^u$. Normally distributed random variable with mean 0.0, and variance s_u^2. Values for s_u^2 were 0, 0.03, and 0.10.
α, β	Parameters for the Ricker spawner-recruit model.
α_o, β_o	Parameter values used in simulations (geometric mean values).

Random variation or error was incorporated in two ways. Annual harvest rate h, environmental factor v, and escapement error factor u were normally distributed random variables (see preceding text table), while in most simulations the age-at-maturity schedule for year-class i (m_{i2}, m_{i3}, m_{i4}, f_{i3}, f_{i4}) was randomly chosen from among five alternative schedules. The variation in h represented random error in estimates of h.

Six sets of age-at-maturity schedules were used to evaluate the effect of different age structures of spawners (Table 1). Differences between the sexes were subjective, based on the observation that females tend to mature later in life than do males (e.g. see

TABLE 1. Alternative sets of age-at-maturity schedules used in simulations. m_j = proportion of male progeny that would mature at age j if there were no harvest; f_j = proportion of female progeny that would mature at age j if there were no harvest; p_j = mean proportion of spawners that are age j when the harvest fraction is 0.65 (no mark) or 0.75 (marked with an asterisk).

Set	m_2	m_3	m_4	f_3	f_4	p_2	p_3	p_4
A	0.15	0.30	0.55	0.23	0.77			
	0.20	0.36	0.44	0.34	0.66			
	0.25	0.50	0.25	0.63	0.37			
	0.35	0.50	0.15	0.77	0.23			
	0.07	0.83	0.10	0.80	0.20	0.29	0.53	0.18
B	0.15	0.30	0.55	0.23	0.77			
	0.20	0.36	0.44	0.34	0.66			
	0.25	0.25	0.50	0.37	0.63			
	0.35	0.15	0.50	0.23	0.77			
	0.07	0.10	0.83	0.20	0.80	0.28	0.33	0.39
C	0.05	0.40	0.55	0.25	0.75			
	0.01	0.35	0.64	0.18	0.82			
	0.02	0.23	0.75	0.12	0.88			
	0.10	0.55	0.35	0.47	0.53			
	0.10	0.45	0.45	0.32	0.68	0.08	0.45	0.47
D	0.00	0.35	0.65	0.23	0.77			
	0.00	0.45	0.55	0.34	0.66			
	0.00	0.67	0.33	0.63	0.37			
	0.00	0.77	0.23	0.77	0.23			
	0.00	0.89	0.11	0.80	0.20	0.00	0.73	0.27
E	0.00	0.50	0.50	0.32	0.68			
	0.00	0.61	0.39	0.47	0.53			
	0.00	0.23	0.77	0.12	0.88			
	0.00	0.35	0.65	0.18	0.82			
	0.00	0.42	0.58	0.25	0.75	0.00	0.49	0.51
F	0.13	0.46	0.41	0.40	0.60	0.26*	0.54*	0.20*

Ricker 1981; Hankin and Healey 1986). When harvest fraction (H) was 0.65, sets *A* and *B* mimicked the recent age structures of chinook salmon from the Klamath and Sacramento rivers, California (Reisenbichler 1986). Various deviations from sets *A* and *B* were introduced in other sets. Set *C* resulted in a smaller proportion of grilse than occurred with the previous sets, and 3- and 4-year-old spawners were almost equally abundant. Set *D* was similar to set *A*, and set *E* was similar to set *C*. except that no fish matured at age 2. Simulations with sets *D* and *E* approximated situations where grilse occur but are counted separately from older spawners and the numbers of grilse are used only to estimate recruitment, not the number of parents.

Some simulations using age-at-maturity set *A* were run with $H = 0.55$ or $H = 0.75$. The different values of H resulted in different age compositions for spawners, e.g. the proportion of spawners that were age 2 ($p_{\bullet 2}$) was 0.22, age 3 ($p_{\bullet 3}$) was 0.51, and age 4 ($p_{\bullet 4}$) was 0.26 for set *A* with $H = 0.55$; and $p_{\bullet 2} = 0.40\ p_{\bullet 3} = 0.47$, and $p_{\bullet 4} = 0.13$ for set *A* with $H = 0.75$. The $p_{\bullet i}$ values for $H = 0.55$ were similar to those for $H = 0.65$; however, the $p_{\bullet i}$ values for $H = 0.75$ were substantially different. Age-at-maturity set *F*, with $H = 0.75$, gave age compositions that were similar to age compositions for set *A* with $H = 0.65$. Set *F* consisted of a single age-at-maturity schedule.

Each run of the model was based on one of the sets of age-at-maturity schedules from Table 1, and on assigned values for the spawner–recruit parameters α and β, the harvest fraction H, and the variances for error in estimating escapement ($s_u{}^2$), annual harvest rate ($s_h{}^2$), and environmental variation ($s_v{}^2$). Mean values calculated for the age-at-maturity parameters m_{ij} and f_{ij} were used to compute the annual harvest rate h consistent with the assigned value for harvest fraction. Since harvest fraction is the proportion of recruits from a year-class that is harvested,

$$H = [h(1 - m_{2\bullet}/2)R + h(1 - h)(m_{4\bullet}/2 + f_{4\bullet}/2)R]/R$$

where $(1 - m_{2\bullet}/2)R$ is the number of 2-year-old progeny that do not mature at age 2 (and are therefore available to the fishery during their third year of life), and $(1 - h)(m_{4\bullet}/2 + f_{4\bullet}/2)R$ is the number of recruits that did not mature at age 2 or age 3 and were not harvested during their third year of life. The $m_{2\bullet}$, $m_{4\bullet}$, and $f_{4\bullet}$ are divided by 2 because 50% of the progeny are male. Rearranging the above equation gives the quadratic equation $0 = bh^2 + ch + d$, where $b = m_{4\bullet}/2 + f_{4\bullet}/2$, $c = -(1 - m_{2\bullet}/2 + m_{4\bullet}/2 + f_{4\bullet}/2)$, and $d = H$. The value for h corresponding to a given value of H was obtained by solving this equation.

The number of age j males from the i'th year-class that spawn in year $(i + j)$ was

$$(1)\quad B_{i2} = m_{i2}R_i/2$$

or

$$(2)\quad B_{ij} = m_{ij}R_i/2 \prod_{k=3}^{j} (1 - h_{i+k}),\ j = 3, 4,$$

and the number of age j females from the i'th year-class that spawn in year $(i + j)$ was

$$(3)\quad G_{ij} = f_{ij}R_i/2 \prod_{k=3}^{j} (1 - h_{i+k}),\ j = 3, 4.$$

Accordingly, the number of female spawners in year i was

$$(4)\quad F_i = G_{i-3,3} + G_{i-4,4}$$

the number of male spawners in year i was

$$M_i = B_{i-2,2} + B_{i-3,3} + B_{i-4,4}$$

and the total number of spawners in year i was

$$(5) \quad T_i = F_i + M_i.$$

The actual spawner-recruit relation used in the model was:

$$(6) \quad R_i = \alpha' F_i e^{(-\beta' F_i + v)},$$

where $\alpha' = \alpha_0/w$, B^1 β_0/w, and $w =$ the expected proportion of female spawners at equilibrium. The value for w was obtained by using the mean values for the age-at-maturity parameters in equations (1) – (3) and dividing the expected number of female spawners (equation [4]) by the expected total number of spawners (equation [5]). The estimated or "observed" number of spawners in year i was the actual number times an error factor, $E_i = T_i e^u$.

The value used most often for s_v^2 was 0.10, after Walters and Ludwig (1981); the effect of greater environmental variation ($s_v^2 = 0.20$ or 0.50) was also examined. For $s_v^2 = 0.10$, 95 % of the values for R_i lie between $0.54\bar{R}_i$ and $1.86\bar{R}_i$, where $\bar{R}_i$ is the value obtained from equation (6) with $v = 0$; for $s_v^2 = 0.20$, the 95 % limits are $0.41\bar{R}_i$ and $2.41\bar{R}_i$; and for $s_v^2 = 0.50$, the 95 % limits are $0.25\bar{R}_i$ and $4.03\bar{R}_i$.

The value used most often for s_h^2 was 0.005. For h with a Gaussian (normal) distribution and a mean of 0.5, the approximate 95 % confidence interval is (0.35, 0.65) when $s_h^2 = 0.005$; the 95 % limits are 0.26 and 0.74 when $s_h^2 = 0.015$ — the alternative value used in simulations. Random values for h that exceeded 0.95 were reduced to 0.95.

The value used most often for s_u^2 was 0.03, after Reisenbichler (1986). Other values considered were $s_u^2 = 0$ and 0.10. For $s_u^2 = 0.10$, 95 % of the E_i lie between $0.54T_i$ and $1.86T_i$; and for $s_u^2 = 0.03$, the 95 % limits are $0.71T_i$ and $1.4T_i$. The number of year-classes in most simulations was 10 because most of the spawner–recruit relations for California were based on data from about 10 year-classes. Other simulations were run with 18 or 20 year-classes.

The model was adapted for use on a computer and was coded in Fortran 77 (Reisenbichler 1986, Appendix D). The numbers of spawners for the first four years were random values from a normal distribution with mean Q and variance $Q/4$, where Q was the equilibrium number of spawners for the assigned value of H,

$$Q = \log_e (\alpha_o(1 - H)/\beta_o)$$

from Ricker (1975, p. 347). From year 5 on, the numbers of recruits were calculated as described earlier. The simulation continued through year 35 and escapements from the last ($y + 4$) years were used to estimate spawner–recruit parameters, where y was the number of year-classes.

The numbers of recruits for each year-class were estimated in two steps when annual age and sex composition data were not used. First, I estimated the number of fish that would have spawned in each stream if there had been no fishing (later referred to as estimates of recruitment by escapement year)

$$R_{e,i} = E_i/(1 - H),$$

where $R_{e,i}$ is the estimated number of fish that would have spawned in year i, E_i is the estimated number of spawners in year i, and H is the harvest fraction. Harvest fraction was not adjusted for noncatch fishing mortality (fish that were killed by the fishery but were not harvested; Ricker 1976) or natural mortality (fish that would have died of natural causes before spawning if they had not been caught).

The second step in estimating the number of recruits was to use approximate age compositions to compute recruitment by brood, R_b, from the R_e' s:

$$R_{b,i} = k_j R_{e,i+j},$$

where the k_j are "age composition weights" described below. Regression of $\log_e (R_{b,i}/S_i)$ on S_i yielded estimates of the parameters for the Ricker model, $R = \alpha S e^{-\beta S}$. Data points were omitted from the analysis if the absolute value of the studentized residual exceeded 2.0. The estimated values for the parameters were compared with the actual values used in the simulation; the difference between estimated and actual values was the bias. Estimates for α were computed as AM (arithmetic mean; Ricker 1975, p. 275) values because environmental variation had less affect on bias for AM values than for GM (geometric mean) values. AM values of α were obtained from GM values according to the relation $\log_{10} (\mathrm{AM/GM}) = 0.217s^2 (y-1)/y$ where s^2 was s_v^2 for α_o or s^2_{curve} (the mean variance of the $\log_e R$ from the fitted model) for α, and y was the number of year-classes.

The procedures for estimating spawner–recruit parameters were modified when age and sex compositions were estimated from random samples of n spawners each year. The estimates for the proportion of spawners that were age 2 (p_{i2}), age 3 (p_{i3}), or female (w_i) were obtained by randomly sampling (with replacement) n times from a uniform (0,1) frequency distribution. The proportion of samples with values less than or equal to the actual value for a particular parameter was taken as the estimate for that parameter. The value for p_{i4} was $1 - p_{i2} - p_{i3}$. The age composition data were used to calculate escapements by year-class, which were divided by $(1 - H)$ to obtain estimates of recruitment for each year-class. Estimated parameters were calculated for only female spawners in these simulations, and therefore were not directly comparable to parameter values estimated without annual age and sex composition data.

Results

The simulations showed that estimates of α and β are imprecise (have large standard deviations) and are often highly biased (i.e. large discrepancy between the mean of the $\hat{\alpha}$ from 200 replications and the value of α actually used in the simulation) when age and sex compositions are unknown: estimates of α were usually too high for small α_0 and too low for large α_0 (Fig. 2), while estimates of β were usually too high for small α_0 (extremely so for $\alpha_0 = 3.0$) and too low for large α_0 (Table 2). The bias for estimates of α was substantially reduced when age 2 fish were eliminated from age-at-maturity sets where they had composed a quarter of the population (Fig. 3); precision (indicated by the stan-

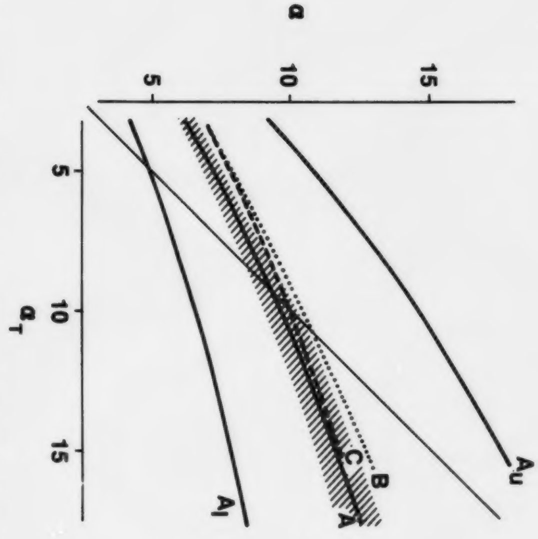

FIG. 2. Mean $\hat{\alpha}$ from simulations with different age-at-maturity sets when $s_u^2 = 0.03$, $s_v^2 = 0.10$, $s_h^2 = 0.005$, $H = 0.65$, and simplified age composition weights were used. Line *A* represents the antilog of the mean $\log_e \hat{\alpha}$ from 200 replicate simulations of 10 year-classes each, with age-at-maturity set *A*. A_l and A_u are the antilogs of the mean $\log_e \hat{\alpha}$ (from line *A*) minus and plus, respectively, one standard deviation of the $\log_e \hat{\alpha}$. Lines *B* and *C* represent the antilog of the mean $\log_e \hat{\alpha}$ from 200 replicate simulations of 10 year-classes each, with age-at-maturity set *B*, and *C*, respectively. Light solid line shows perfect relation (no bias) between estimated values and α_T. Shaded area indicates 95 % confidence interval for line *A*; confidence intervals for B and C were similar. Age composition weights were $k_2 = 0$, $k_3 = 1$, and $k_4 = 0$ for age-at-maturity set *A*, and $k_2 = 0$, $k_3 = 0.5$, and $k_4 = 0.5$ for age-at-maturity sets *B* and *C*.

TABLE 2. Results from Monte Carlo simulations when age and sex compositions were not available. α_0, β_0 = parameter values used in simulations; α_T = AM value for α_0 (Ricker 1975, p. 274); Years = number of year-classes; Mat. set = age-at-maturity set from Table 1; $\overline{\alpha}$ = geometric mean of the $\hat{\alpha}$ from 200 replications; $MSD_{\hat{\alpha}}$ = antilog of the standard deviation of the $\log_e \hat{\alpha}$; $\overline{\beta}$ = mean of the $\hat{\beta}$; $SD_{\hat{\beta}}$ = standard deviation of the $\hat{\beta}$; s^2_{curve} = mean variance of the $\log_e R$ from the fitted model; k_2, k_3, k_4 = age composition weights for computing R_b from R_e; $s_h^2 = 0.005$; $s_u^2 = 0.03$; $k_2 = 0$.

Parameter or variable	Simulation																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
α_0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	4.3	5.5	5.5	5.5	7.0	11.0	11.0	11.0	14.9	14.9	14.9	14.9	14.9	14.9	14.9
β_0 (×100)	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.05	0.05	0.05	0.05	0.01	0.07	0.07	0.07	0.73	0.73	0.73	0.73	0.73	0.73	0.73
s_v^2	0.10	0.10	0.10	0.10	0.20	0.20	0.50	0.10	0.10	0.10	0.20	0.10	0.10	0.10	0.20	0.10	0.10	0.10	0.10	0.20	0.20	0.50
Years	10	10	10	10	10	18	10	10	10	10	10	10	10	10	10	10	10	10	10	10	18	10
Mat. set	A	D	B	E	A	A	A	A	A	D	A	A	A	D	A	A	D	B	E	A	A	A
k_3	1.0	1.0	0.5	0.5	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	0.5	1.0	1.0	1.0
k_4	—	—	0.5	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	0.5	0.5	—	—	—
α_T	3.1	3.1	3.1	3.1	3.3	3.3	3.8	4.5	5.8	5.8	6.1	7.4	11.6	11.6	12.2	15.6	15.6	15.6	15.6	16.4	16.4	18.7
$\overline{\alpha}$	6.2	5.6	8.1	6.9	6.5	5.9	7.3	7.1	7.6	7.4	8.0	8.5	10.3	11.2	10.8	11.8	13.5	11.3	12.1	12.5	12.1	14.1
$MSD\hat{\alpha}$	1.48	1.41	1.40	1.33	1.52	1.35	1.68	1.49	1.50	1.46	1.53	1.50	1.48	1.54	1.52	1.50	1.50	1.46	1.40	1.53	1.39	1.65
$\overline{\beta}$ (×100)	0.18	0.13	0.20	0.16	0.17	0.13	0.15	0.13	0.08	0.07	0.08	0.13	0.67	0.68	0.67	0.61	0.65	0.57	0.59	0.62	0.59	0.60
$SD_{\hat{\beta}}$ (×100)	0.16	0.11	0.13	0.09	0.18	0.11	0.20	0.07	0.04	0.03	0.04	0.05	0.23	0.24	0.24	0.19	0.19	0.17	0.15	0.20	0.15	0.21
s^2_{curve}	0.19	0.27	0.05	0.07	0.23	0.22	0.42	0.18	0.20	0.23	0.20	0.16	0.17	0.23	0.21	0.18	0.24	0.08	0.09	0.22	0.22	0.32

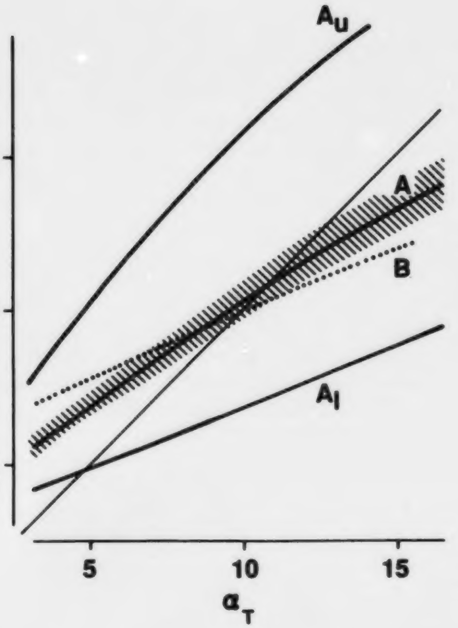

FIG. 3. Mean $\hat{\alpha}$ from simulations when there were no grilse, and $s_u^2 = 0.03$, $s_v^2 = 0.10$, $s_h^2 = 0.005$, $H = 0.65$, and simplified age composition weights were used. Line *A* represents the antilog of the mean $\log_e\hat{\alpha}$ from 200 replicate simulations of 10 year-classes each, with age-at-maturity set *D*. A_l and A_u are the antilogs of the mean $\log_e\hat{\alpha}$ (from line *A*) minus and plus, respectively, one standard deviation of the $\log_e\hat{\alpha}$. Lines *B* represents the antilog of the mean $\log_e\hat{\alpha}$ from 200 replicate simulations of 10 year-classes each, with age-at-maturity set *E*. Light solid line shows perfect relation (no bias) between estimated values and α_T. Shaded area indicates 95 % confidence interval for line *A*; the confidence interval for *B* was similar. Age composition weights were $k_2 = 0$, $k_3 = 1$, and $k_4 = 0$ for age-at-maturity set *D*, and $k_2 = 0$, $k_3 = 0.5$, and $k_4 = 0.5$ for age-at-maturity set *E*.

dard deviation) for both parameters, and the bias in estimates of β were somewhat improved (in Table 2, compare within each of the following pairs of simulations: 1–2, 3–4, 9–10, 13–14, 16–17, and 18–19).

Increasing the number of year-classes from 10 to 18 reduced bias and increased precision for estimated parameters, but substantial bias remained (in Table 2, compare between simulations 5 and 6 and between 20 and 21). The bias in estimating α was affected by changes in age composition weights (Table 3) or age-at-maturity set (Fig. 2). The smallest bias for age-at-maturity set A (where age 3 fish were the most abundant age class and composed, on the average, 53 % of the spawners) was observed when age 2 and age 4 fish were ignored and all fish were considered as age 3; the bias was greatest when all three ages of fish were included (Table 3).

TABLE 3. Estimated spawner-recruit parameters from Monte Carlo simulations with age-at-maturity set *A* (from Table 1) and different age composition weights. α_0, β_0 = parameter values used in the simulation; α_T = AM value for α_0 (Ricker 1975, p. 274); $\overline{\alpha}$ = geometric mean of the $\hat{\alpha}$ from 200 replications; $\underline{\text{MSD}}_{\hat{\alpha}}$ = antilog of the standard deviation of the $\log_e\hat{\alpha}$; $\overline{\beta}$ = mean of the $\hat{\beta}$; $\text{SD}_{\hat{\beta}}$ = standard deviation of the $\hat{\beta}$; s^2_{curve} = mean variance of the $\log_e R$ from the fitted model. Each simulation produced spawner-recruit data for 10 year-classes. $s_v^2 = 0.10$; $s_u^2 = 0.03$; $s_h^2 = 0.005$; $H = 0.65$.

Parameter or variable	Simulation					
	1	2	3	4	5	6
α_0	3.0	3.0	3.0	14.9	14.9	14.9
β_0 (×100)	0.01	0.01	0.01	0.73	0.73	0.73
k_2	—	—	0.25	—	—	0.25
k_3	1.0	0.67	0.50	1.0	0.67	0.50
k_4	—	0.33	0.25	—	0.33	0.25
a_T	3.1	3.1	3.1	15.6	15.6	15.6
$\overline{\alpha}$	6.2	7.0	7.6	11.8	11.3	10.9
$\underline{\text{MSD}}_{\hat{\alpha}}$	1.48	1.43	1.33	1.50	1.43	1.32
$\overline{\beta}$ (×100)	0.18	0.20	0.20	0.61	0.59	0.57
$\text{SD}_{\hat{\beta}}$ (×100)	0.16	0.16	0.13	0.19	0.17	0.13
s^2_{curve}	0.19	0.10	0.07	0.18	0.11	0.08

TABLE 4. Estimated spawner-recruit parameters from Monte Carlo simulations with different values for s_u^2. α_0, β_0 = parameter values used in simulation; α_T = AM value for α_0 (Ricker 1975, p. 274); $\overline{\alpha}$ = geometric mean of the $\hat{\alpha}$ from 200 replications; $\underline{\text{MSD}}_{\hat{\alpha}}$ = antilog of the standard deviation of the $\log_e\hat{\alpha}$; $\overline{\beta}$ = mean of the $\hat{\beta}$; $\text{SD}_{\hat{\beta}}$ = standard deviation of the $\hat{\beta}$; s^2_{curve} = mean variance of the $\log_e R$ from the fitted model. Each simulation produced spawner-recruit data for 10 year classes. $s_v^2 = 0.10$; $s_h^2 = 0.005$; The age-at-maturity set was *A* from Table 1. Age composition weights were $k_2 = 0$, $k_3 = 1.0$, $k_4 = 0$.

Parameter or variable	Simulation					
	1	2	3	4	5	6
α_0	3.0	3.0	3.0	14.9	14.9	
β_0 (×100)	0.01	0.01	0.01	0.73	0.73	0.73
s_u^2	0.10	0.05	0.03	0.10	0.05	0.03
a_T	3.1	3.1	3.1	15.6	15.6	15.6
$\overline{\alpha}$	7.2	6.5	6.2	11.7	11.7	11.8
$\underline{\text{MSD}}_{\hat{\alpha}}$	1.61	1.53	1.48	1.51	1.51	1.50
$\overline{\beta}$ (×100)	0.20	0.18	0.18	0.57	0.60	0.61
$\text{SD}_{\hat{\beta}}$ (×100)	0.19	0.17	0.16	0.20	0.20	0.19
s^2_{curve}	0.27	0.22	0.19	0.25	0.20	0.18

Increasing environmental variance or error variance increased the bias in estimates of α when $\alpha_0 = 3$, but had little effect on bias when $\alpha_0 = 14.9$, and had little effect on estimates for β (in Table 2, compare among simulations 1, 5, and 7, and among 16, 20, and 22; Table 4). Of course, precision declined as these variances increased. Walters and Ludwig (1981) observed similar results for single-age-at-maturity populations: measurement error caused the greatest bias in estimated

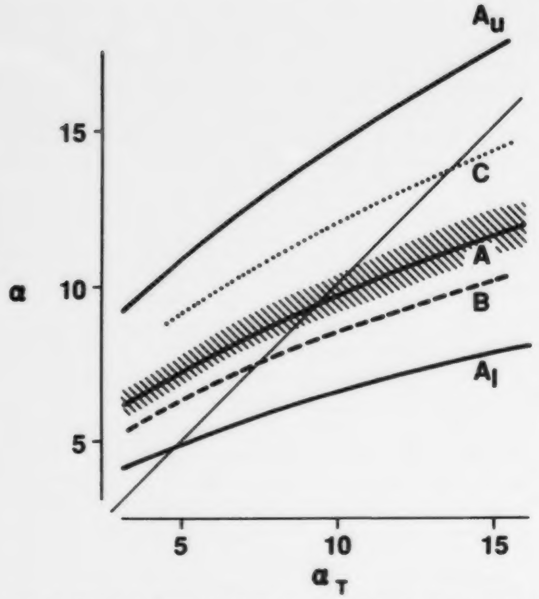

FIG. 4. Mean $\hat{\alpha}$ from simulations when harvest fraction (H) was 0.65 (line *A*), 0.55 (line *B*), and 0.75 (line *C*), and $s_u^2 = 0.03$, $s_v^2 = 0.10$, and $s_h^2 = 0.005$. Age-at-maturity set *A* (from Table 1) was used for lines *A* and *B*, and set *F* was used for line *C*. Line *A*, *B*, and *C* represent the antilog of the mean $\log_e\hat{\alpha}$ from 200 replicate simulations of 10 year-classes each. A_l and A_u are the antilogs of the mean $\log_e\hat{\alpha}$ (from line *A*) minus and plus, respectively, one standard deviation of the $\log_e\hat{\alpha}$. Light solid line shows perfect relation (no bias) between estimated values and α_T. Shaded area indicates 95% confidence interval for line *A*; confidence intervals for B and C were similar. Age composition weights were $k_2 = 0$, $k_3 = 1$, and $k_4 = 0$.

spawner–recruit parameters for populations with low productivity.

Increasing harvest fraction from 0.55 to 0.75 (decreasing the mean number of spawners) substantially increased bias (Fig. 4). Increasing the variance in harvest rate (s_h^2) increased $\hat{\beta}$ and the standard deviation of $\hat{\beta}$ ($SD_{\hat{\beta}}$) when $\alpha_o = 3$, and increased s^2_{curve} (the mean variance of the $\log_e R$ from the fitted model), but had little effect on $\hat{\alpha}$ (variable and parameter values from simulations 1 and 16, Table 2):

s_h^2	$\hat{\alpha}$	$MSD_{\hat{\alpha}}$	$\hat{\beta}$	$SD_{\hat{\beta}}$	s^2curve
		Simulation 1 — $\alpha_o = 3$, $\beta_o = 0.0001$			
0.0	6.2	1.46	0.0016	0.0015	0.17
0.005	6.2	1.48	0.0018	0.0016	0.19
0.015	6.1	1.46	0.0022	0.0025	0.25
		Simulation 16 — $\alpha_0 = 14.9$, $\beta_o = 0.0073$			
0.0	11.4	1.52	0.0059	0.0020	0.15
0.005	11.8	1.50	0.0061	0.0019	0.18
0.015	12.1	1.49	0.0062	0.0020	0.23

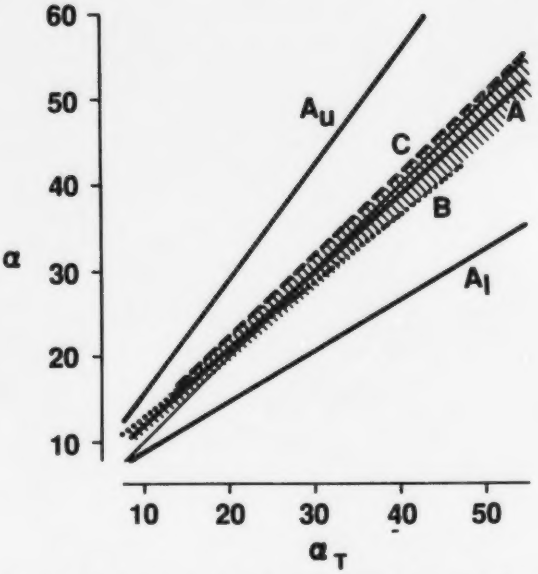

FIG. 5. Mean $\hat{\alpha}$ from simulations when $s_u^2 = 0.03$, $s_v^2 = 0.10$, $s_h^2 = 0.005$, and age and sex compositions of spawners were estimated or known each year. Line *A* represents the antilog of the mean $\log_e\hat{\alpha}$ from 200 replicate simulations of 10 year-classes each, with estimated age and sex compositions from samples of 100 fish and $H = 0.65$. A_l and A_u are the antilogs of the mean $\log_e\hat{\alpha}$ (from line *A*) minus and plus, respectively, one standard deviation of the $\log_e\hat{\alpha}$. Lines *B* and *C* represent the antilog of the mean $\log_e\hat{\alpha}$ from 200 replicate simulations of 10 year-classes each, when age and sex compositions were know and $H = 0.55$ (line *B*) and $H = 0.75$ (line *C*). Age-at-maturity set *A* (from Table 1) was used for lines *A* and *B*; set *F* was used for line *C*. Light solid line shows perfect relation (no bias) between estimated values and α_T. Shaded area indicates 95% confidence interval for line *A*; confidence intervals for *B* and *C* were similar.

Increasing s_h^2 should have increased the range in numbers of spawners, and the increased range probably explains the improved accuracy in parameter estimates despite increased error in estimating recruitments (i.e. increased discrepancy between the actual harvest fraction and *H*).

Rejecting outliers had little effect on the mean values for $\hat{\alpha}$ and $\hat{\beta}$ but did reduce s^2_{curve} (variable and parameter values from simulations 1 and 16, Table 2):

	$\hat{\alpha}$	$MSD_{\hat{\alpha}}$	$\hat{\beta}$	$SD_{\hat{\beta}}$	s^2_{curve}
		Simulation 1 — $\alpha_o = 3$, $\beta_o = 0.0001$			
Keep outliers	6.2	1.44	0.0017	0.0015	0.23
Reject outliers	6.3	1.48	0.0018	0.0016	0.19
		Simulation 16 — $\alpha_o = 14.9$, $\beta_o = 0.0073$			
Keep outliers	11.9	1.43	0.0061	0.0017	0.22
Reject outliers	11.8	1.50	0.0061	0.0019	0.18

Bias in estimates for α (Fig. 5) and β was greatly reduced when annual age and sex composition data were used, except that estimates of β remained high and did not approximate β for small α (i.e. α near 3.0; Table 5). Bias declined as the number of fish sampled for age and sex composition increased (in Table 5, compare among simulations 2–5 and 16–18), but even with samples of only 50 fish, parameter estimates were much improved over those obtained without age and sex composition data. Of course, precision for $\hat{\alpha}$ and $\hat{\beta}$ increased with the number of year-classes (in Table 5, compare among simulations 4, 9, and 10, and among 17, 22, and 23). Age-at-maturity set (Table 5) and harvest fraction (Fig. 5) affected parameter estimates much less than when age and sex composition data were not available (Table 2; Fig. 4).

Discussion

Walters and Ludwig (1981), using a model without age structuring, indicated that the numbers of spawners must be estimated with $s_u^2 \leq 0.05$ to avoid substantial bias in estimated spawner–recruit parameters. The results from simulations presented here (for species with multiple ages at maturity) have shown that lack of annual age and sex composition data also causes substantial bias and, for $s_u^2 \leq 0.10$, resulted in greater bias than did error in estimating escapement. Furthermore, bias varied with age structure of the population, productivity of the population, and harvest rate. Environmental variation caused low precision (large standard deviation) for parameters estimated with or without age and sex composition data; however, precision was substantially improved when age and sex composition data were available. Age and sex composition data can also provide other benefits: with these data managers can apply age-structured reproduction models (in contrast to standard spawner–recruit relations such as the Ricker [1954] model) to better understand the effects of harvest on salmon populations and to more closely approach "optimum" production (e.g. see Hankin and Healey 1986).

Lack of annual age and sex composition estimates seemed to be the most serious deficiency in the data for California chinook salmon (Reisenbichler 1986). Error in parameter estimates caused by imprecise (but presumably unbiased) estimates of harvest fraction were of much less consequence. As expected, counting grilse separately from older spawners (partial age compositions) resulted in less bias for estimated parameters than when no age composition data were available. Nevertheless, the mean bias was still much greater with these partial age compositions than it would have been if complete age composition data had been available.

Shifts in estimated spawner–recruit relations for natural populations of salmon have generally involved at least twofold changes (usually at least 50 % reductions)

TABLE 5. Estimated spawner–recruit parameters from Monte Carlo simulations when age and sex compositions were estimated each year and $\alpha_0 = 3.0$ and $\beta_0 = 0.0001$ (before adjusting for only female spawners). Years = number of year classes; Mat. set = age-at-maturity set from Table 1; N = number of spawners sampled each year for age and sex determination; α_T = AM value for α_0 when only female spawners are considered; β_T = value for β_0 when only female spawners are considered; $\bar{\alpha}$ = geometric mean of the $\hat{\alpha}$ from 200 replications; $\mathrm{MSD}_{\hat{\alpha}}$ = antilog of the standard deviation of the $\log_e\hat{\alpha}$; $\bar{\beta}$ = mean of the $\hat{\beta}$; $\mathrm{SD}_{\hat{\beta}}$ = standard deviation of the $\hat{\beta}$; s^2_{curve} = mean variance of the $\log_e R$ from the fitted model; $s_h^2 = 0.005$.

Parameter	Simulation																							
or variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
α_0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	3.0	11.0	11.0	11.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0	20.0
β_0 (×100)	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.07	0.07	0.07	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10
s_v^2	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.20	0.10	0.10	0.20	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.20
Years	10	10	10	10	10	10	10	10	20	6	10	10	20	10	10	10	10	10	10	10	10	20	6	10
s_u^2	0.10	0.03	0.03	0.03	0.03	0.03	0.03	0	0.03	0.03	0.03	0.03	0.03	0.03	0.10	0.03	0.03	0.03	0.03	0.03	0	0.03	0.03	0.03
Mat. set	A	A	A	A	A	C	B	A	A	A	A	A	A	A	A	A	A	A	C	B	A	A	A	A
N	∞[a]	∞[a]	500	100	50	100	100	∞[a]	100	100	100	100	100	100	∞[a]	∞[a]	100	50	100	100	∞[a]	100	100	100
α_T	8.2	8.2	8.2	8.2	8.2	7.1	7.7	8.2	8.2	8.2	8.6	30.1	30.1	31.7	54.8	54.8	54.8	54.8	47.0	51.1	54.8	54.8	54.8	57.6
β_T (×100)	0.03	0.03	0.03	0.03	0.03	0.02	0.03	0.03	0.03	0.03	0.03	0.18	0.18	0.18	0.26	0.26	0.26	0.26	0.22	0.26	0.26	0.26	0.26	0.26
$\bar{\alpha}$	11.7	9.8	10.1	10.6	11.4	10.6	12.7	9.2	10.6	10.8	11.0	29.5	30.0	31.3	49.2	51.6	52.0	50.9	41.9	45.3	54.0	50.3	52.0	48.6
$\mathrm{MSD}\hat{\alpha}$	1.38	1.30	1.30	1.34	1.36	1.44	1.48	1.27	1.23	1.62	1.33	1.41	1.25	1.47	1.55	1.43	1.48	1.48	1.51	1.56	1.33	1.27	1.69	1.58
$\bar{\beta}$ (×100)	0.22	0.13	0.15	0.18	0.20	0.21	0.23	0.12	0.16	0.16	0.15	0.18	0.18	0.18	0.23	0.25	0.25	0.25	0.21	0.23	0.26	0.24	0.24	0.24
$\mathrm{SD}_{\hat{\beta}}$ (×100)	0.29	0.23	0.24	0.26	0.26	0.29	0.24	0.21	0.16	0.45	0.33	0.46	0.33	0.05	0.06	0.05	0.06	0.06	0.05	0.06	0.03	0.04	0.08	0.07
s^2_{curve}	0.22	0.15	0.16	0.18	0.18	0.16	0.15	0.12	0.17	0.19	0.26	0.15	0.15	0.24	0.23	0.17	0.18	0.20	0.17	0.16	0.12	0.18	0.24	0.25

[a] Age and sex compositions were not estimated; the actual values were used.

in productivity or carrying capacity (see above), perhaps because spawner–recruit analyses are unlikely to detect smaller changes. In light of the magnitude of the standard deviations for the estimated parameters (from simulations), it seems unlikely that even twofold changes could be detected; however, estimates of α and β are jointly distributed (Fig. 6), allowing much greater sensitivity for detecting differences than that indicated by the variance of either parameter considered separately (Johnson and Wichern 1982). The nonzero covariance between estimates for α and β provided for a joint confidence interval (an ellipse) for $(\hat{\alpha}, \hat{\beta})$ that was much smaller than the confidence rectangle formed by the separate confidence intervals for the two parameters.

To evaluate the sensitivity of spawner–recruit relations for detecting the effects of environmental change, I plotted the estimated spawner–recruit parameters from simulations (using 10 year-classes with annual estimates of age and sex compositions) with 0 %, 33 %, and 50 % reductions in α_0 and 0 %, 50 %, and 100 % increases in β_0. The initial value for α was 9, perhaps typical for chinook salmon from British Columbia to California (Reisenbichler 1987); the initial value for β was arbitrarily chosen as 0.007; and $s_u^2 = 0.03$, $s_h^2 = 0.005$, and $H = 0.65$. Estimated parameters for the initial spawner–recruit relation substantially overlapped those reflecting a 33 % reduction (1.5-fold shift) in α_0 when environmental variation was low (0.1; Fig. 6); overlap before and after a 50 % reduction (twofold shift) in α_0 was much less when environmental variation was high (0.5; Fig. 7), and was very small when environmental variation was low (0.1; Fig. 8). The results from 50 and 100 % increases in β_0 matched those from 33 and 50 % reductions in α_0, respectively, and are not shown here.

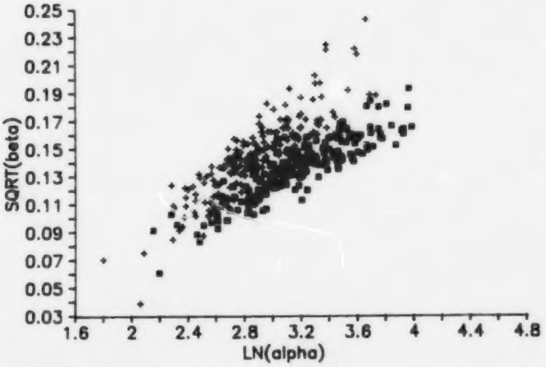

FIG. 6. Estimated values for α and β from simulations when $\alpha_0 = 9$, $\beta_0 = 0.007$ (squares) and when $\alpha_0 = 6$, $\beta_0 = 0.007$ (+'s), and age and sex composition are estimated each year from a sample of 100 fish. $s_v^2 = 0.10$, $s_u^2 = 0.03$, $s_h^2 = 0.005$, and age-at-maturity set was *A* from Table 1.

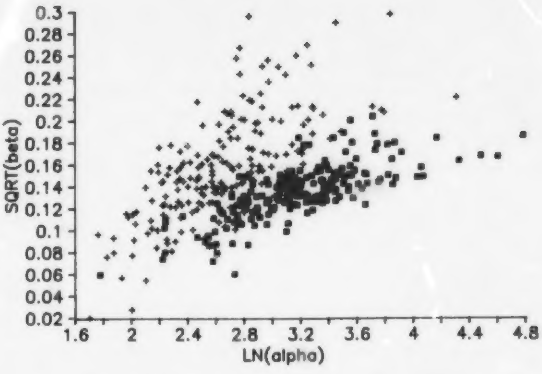

FIG. 7. Estimated values for α and β from simulations when $\alpha_0 = 9$, $\beta_0 = 0.007$ (squares) and when $\alpha_0 = 4.5$, $\beta_0 = 0.007$ (+'s), and age and sex composition are estimated each year from a sample of 100 fish. $s_v^2 = 0.50$, $s_u^2 = 0.03$, $s_h^2 = 0.005$, and age-at-maturity set was *A* from Table 1.

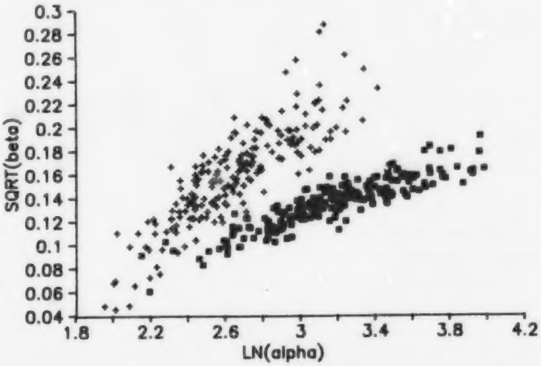

FIG. 8. Estimated values for α and β from simulations when $\alpha_0 = 9$, $\beta_0 = 0.007$ (squares) and when $\alpha_0 = 4.5$, $\beta_0 = 0.007$ (+'s), and age and sex composition are estimated each year from a sample of 100 fish. $s_v^2 = 0.10$, $s_u^2 = 0.03$, $s_h^2 = 0.005$, and age-at-maturity set was *A* from Table 1.

I also used the results from the simulations with $\alpha_0 = 9$ and $\beta_0 = 0.007$ to calculate the smallest true difference between α's that could be detected with only a 5 % chance of a Type I error and with a 20 % chance of a Type II error (Sokal and Rohlf 1969). The difference was a twofold change in α when environmental variation was 0.1 and a threefold change when environmental variation was 0.5. Because the environmental variation experienced by real populations is probably at least 0.1, these minimum detectable differences and the overlap in estimated parameters (Fig. 6–8) support the above contention that spawner–recruit analysis is unlikely to detect less than twofold changes in productivity or carrying capacity.

The unquestionable conceptual value of spawner–recruit relations for evaluating environmental change stands in contrast to their low sensitivity for detecting change and the low precision for estimating the magnitude of change. Although only the Ricker model was evaluated here, the conclusions presented here should apply to spawner–recruit models in general, and to all species of salmon that mature at several ages within the same population. Once accurate estimates of harvest, escapement, and age and sex composition of escapement are forthcoming, the accuracy of estimated spawner–recruit relations and their sensitivity for detecting environmental change can be increased by varying harvest fraction to increase the range of escapements (the costs and benefits of such active adaptive or experimental management have been discussed by Walters [1975; 1981], Walters and Hilborn [1976], Holling [1978], Smith and Walters [1981], and Walters and Ludwig [1987]), and by increasing the number of data points. These means for increasing accuracy, however, may be unlikely to be adopted or may not be feasible — managers have been reluctant to initiate adaptive management, and potential gains from monitoring populations for more years may be offset by other, confounding shifts in spawner–recruit relations. Incorporating environmental factors that are likely to have a large effect on survival (e.g. stream flow, ocean upwelling) into the model, or filtering part of the density-independent variation in survival (Welch 1986), may substantially improve the precision of estimated relations but will usually require longer time series of data. Without such increased precision, however, spawner–recruit analysis is an inexact and insensitive tool for evaluating the effects of environmental change.

Acknowledgements

The manuscript benefited from reviews by R. Burgner, D. Chapman, D. Hankin, S. Hornig, S. Mathews, and R. Whitney. G. Konkel facilitated the work with the computer.

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The Ecology of Fish and Populations: Dealing with Interactions between Levels[1]

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Abstract

SHUTER, B. J., AND H. A. REGIER. 1989. The ecology of fish and populations: dealing with interactions between levels, p. 33–49. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

In principle, the amount of fish habitat in an area should be measurable in terms of the number of individuals that it can support on a sustained basis. However, there are inherent limits to the reliability of such measurements. The nature of these limits must be recognized and dealt with in a consistent and rational fashion if management based on habitat quantification is to function at all. We define the "habitat" of a population as the amount of living space environmentally suitable for its members. Thus reduction in habitat can arise from deterioration in environmental conditions (abiotic and biotic), as well as from the physical elimination of usable space. We assume that quantifying a change in the amount of habitat is functionally equivalent to forecasting how the abundance of a population is affected by a specific change in its environment. This definition permits us to mine the extensive literature on environmental impact assessment for insights into the issue of habitat measurement. Methods of forecasting the effects of environmental changes on fish stocks can be grouped into two broad categories: those based primarily on knowledge of the behavior of individual organisms; those based primarily on knowledge of the behavior of individual stocks. Methods in both categories require some information from at least two levels of biological organization (i.e. individual, population, community) in order to construct a credible forecast. We discuss logical ways for linking such disparate bits of information into a coherent whole. We illustrate the kinds of limitations which inevitably arise from such linkages and show how to deal with them through a small number of well defined trial forecasts which bound likely changes in population abundance. These estimate the maximum and minimum amount of habitat which is likely to be lost given a specific change in environmental conditions.

Résumé

SHUTER, B. J., AND H. A. REGIER. 1989. The ecology of fish and populations: dealing with interactions between levels, p. 33–49. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

En principe, on devrait pouvoir mesurer l'étendue des habitats de poissons dans une region d'après le nombre d'individus qu'ils peuvent accueillir de façon soutenue. Toutefois, il existe des limites inhérentes quant à la fiabilité de ces mesures. Il faut reconnaître la nature de ces limites et en tenir compte de façon constante et rationnelle pour que les techniques de gestion reposant sur la quantification des habitats soient valables. Nous définissons « l'étendue d'un habitat » d'une population comme suit : l'espace qui présente des conditions écologiques favorables à la survie de ses membres. En conséquence, cet espace peut se rétrécir par suite de la détérioration du milieu (conditions abiotiques et biotiques) ainsi que de la perte de zones

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[1] Contribution No. 87-03 of the Ontario Ministry of Natural Resources, Research Section, Fisheries Branch, Box 50, Maple, Ont. L0J 1E0.

utilisables. Nous présumons que le fait de mesurer les changements de l'étendue d'un habitat correspond à prévoir les effets d'une modification précise de l'environnement d'une population sur son abondance. Cette définition nous permet de fouiller les fort nombreuses évaluations des incidences environnementales, afin d'obtenir plus de renseignements sur la question de la quantification des habitats. Les méthodes de prévision des effets des changements écologiques sur les stocks de poissons peuvent être classées dans deux grandes catégories: celles qui reposent principalement sur les connaissances relatives au comportement des individus et celles qui se fondent sur les connaissances au sujet du comportement des stocks particuliers. Que l'on emploie une méthode de l'une ou l'autre des catégories, il faut disposer de certaines données pour au moins deux systèmes biologiques (c.-à-d., les individus, les populations, les communautés) afin de faire des prévisions plausibles. Nous examinons des façons logiques permettant de regrouper ces renseignements fragmentaires pour en former un tout cohérent. Nous décrivons le type de facteurs limitatifs qui surgissent inévitablement lorsqu'on tente d'établir de tels liens, et comment y remédier en effectuant quelques prévisions préliminaires bien définies qui permettent de catégoriser les changements probables quant à l'abondance d'une population. Au cours de ces essais, on estime l'étendue maximale et minimale des habitats qui risquent d'être perdus par suite de changements donnés dans le milieu.

Introduction

Can "salmonid habitat" be defined and measured quantitatively? This was a major issue addressed during the workshop. We approach this question as biologists experienced in environmental impact assessment with non-salmonid species. We assume that the answer is a qualified yes and that the real issues of interest are issues of methodology: how and with what precision can these measurements be made? We draw on our experience with non-salmonids to describe some approaches which may be useful in dealing with this problem.

The habitat of a particular fish population consists of the physico-chemical and biological features that characterize the daily environment of individual population members (Milner et al. 1985). Our objective is to work out procedures for combining these disparate aspects of fish habitat into an estimate of sustainable population size. This will permit deterioration in habitat to be evaluated in terms of a reduction in abundance. This approach hinges on the idea that reliable forecasts of population abundance are possible, a premise which itself is somewhat controversial (Rigler 1982; Walters 1987).

The centerpiece of classical fisheries science is a complete theory of the dynamics of population abundance (Beverton and Holt 1957; Ricker 1975). Critical variables are defined and an elaborate technology has been developed to measure them. However, in its simplest and most widely applied form, this theory takes an essentially "atomic" (after Ravetz 1986) view of aquatic ecosystems: each fish population is an isolated bit of reality which can be understood and defined without detailed reference to the characteristics of either its biotic components (individual population members) or its abiotic and biotic environment. There is no explicit statement of the constraints set on population abundance by the presence of competitors and predators. Similarly, explicit connections linking changes at lower levels of organization (organism/abiotic environment) to changes in population abundance are absent. Yet in most impact assessment situations, it is just these lower level changes which current understanding permits us to predict and then monitor with some confidence.

To cite a recent, high profile example, current technology did permit a credible and relatively unambiguous assessment of the immediate effects of Hudson River power plant development on the mortality of larval striped bass (Barnthouse et al. 1984). However, current theory and technology did not permit an unambiguous assessment of the long-term consequences that additional mortality would have for average population abundance.

Such difficulties have led to the suggestion that impact assessment, based on forecasts of population abundance, is impossible in principle. For example, Rigler (1982) argues that current evolutionary theory demands that we view each individual population as an ephemeral entity, for which the term "long-term" average abundance has no true meaning. He also suggests that current ecological theory views each population as a unique entity, so tightly integrated into its own particular ecosystem, that the data collection program required for a credible "short- term" forecast of population abundance would itself significantly alter the very system under study — the analogy with Heisenberg's uncertainty principle is explicit. Walters et al. (1989) present data consistent with this view. They show that the sensitivity of manipulative experiments at the population level is severely compromised because:

(1) the number of "replicate" populations available for use in such experiments is severely limited,

(2) local uniqueness among potential replicates is so high that within treatment variance does not stabilize.

A complimentary argument (O'Neil et al. 1986) suggests that there is a "natural" hierarchical organization in most ecosystems which does not map directly into the old "levels of organization" concept. For some environmental changes, an analysis of impact at the population level is simply inappropriate: well-founded, unambiguous forecasts of change can only be obtained at some other level in the hierarchy.

However, most impact assessment problems are inexorably drawn towards the population level. Public interest in the aquatic environment will always focus on the fate of individual populations of highly valued species of fish. In the Hudson River example, the fate of striped bass eventually became the primary issue for the assessment effort to deal with, despite the fact that many biologists felt that other impacts within the Hudson River ecosystem were substantial. Thus, we are faced with a conundrum: human interest demands reliable impact assessment on entities (individual population abundances) whose future behavior may be unpredictable in principle.

In this essay, we argue that there are formal techniques for bridging the gap between levels and using all available data to bound likely changes in population abundance. These same techniques should also be useful in forecasting bounds on likely changes in the amount of fish habitat.

Difficulties in Forecasting Population Abundance

All forecasts are generated using a model of how the world works. A typical forecast consists of two parts: (1) specification of a time period for the forecast (forecast length); (2) listing of the changes that occur during that time period. The extent to which the predicted changes are specified can vary widely: specification of direction (e.g. up, down, no change), specification of direction plus bounds on magnitude (e.g. up and $< x$), specification of direction and absolute magnitude (e.g. up and $= x$). Similarly, the forecast length can vary from short to long. We will argue that; (1) the difficulties inherent in forecasting the abundance of individual populations are such that reliable long-term forecasts of absolute abundance are rarely possible and should not be expected; (2) effort should be directed toward predicting the bounds of likely changes in population abundance; (3) short term projections of absolute abundance are useful in the following roles: as tentative predictions of the future; as benchmarks, permitting early detection of unexpected properties of the system being studied.

For a given model, short-term forecasts are generally more reliable than long-term forecasts and broad, qualitative forecasts are more reliable than precise, quantitative forecasts. There are two ways to stretch these limits on forecast reliability: (1) try to maintain reliability by expanding the scope of the forecast model: include more aspects of the world in the model; (2) accept the fact that forecast reliability will be increasingly contingent on a "stability" assumption — the assumption that those aspects of the world not explicitly included in the model will remain unchanged throughout the life of the forecast. This means that, as we demand more of a forecast (in precision or duration), then more aspects of the situation must be explicitly considered in making the forecast. That consideration can take the form of a detailed representational model, attached to the existing forecast model, or it can consist of the stability assumption (SA) listed above.

The nature of this methodological problem becomes clearer as we examine the kinds of models commonly used in generating forecasts. Two distinct approaches to building such models are common in the literature, and have been identified and described by several authors (Table 1). The terminology may vary but the same basic categories are recognized. We will follow Rigler's (1982) scheme, modifying his definitions somewhat to sharpen the contrast between methods:

1) Analytical/explanatory models - simulation models which describe the responses of individuals to environmental variables and evaluate the effects of those responses on population level variables;
2) Empirical models — regression relations which quantify observed associations between population level variables and environmental variables; such models can be based on time series data from a single population or on comparative data from separate populations.

A typical analytical model is built from a small number of variables and a larger number of constants. These constant terms embody those aspects of the world that are not expected to change during the life of the forecast — the SA. The nature of analytical models is such that the constant terms are explicitly identified with abiotic and biotic processes that may be well understood in their own right. Thus, the credibility of the SA can easily be evaluated. As the length of the forecast interval increases, the SA becomes less credible for certain parameters. The only remedy is to explicitly model the processes which underlie those parameters — convert the appropriate constants into a series of new equations built from a new set of variables and constants. Demands for more precise, quantitative forecasts force a similar expansion in the scope of the model. For example, consider an exploited fish population whose productivity is described by a simple surplus production model (Ricker 1975, chap. 13):

$$\begin{array}{l}\text{net biomass produc-}\\ \text{tion by exploited}\\ \text{segment of stock}\end{array} = f\left(\begin{array}{l}\text{biomass of}\\ \text{exploited segment}\end{array}\right)$$

As long as fishermen do not change the age selectivity of their fishing gear, this model can be used to forecast the effects on population abundance of changes in fishing effort. However, such a model cannot be used to forecast the effects of changes in both effort and gear

TABLE 1. Approaches to the modeling of environmental problems.

Labels	Definitions
Data-based/theory-based approaches (Caprariis 1983)	Data-based approach: involves constructing a simple model derived solely from data collected from the particular system of interest.
	Theory-based appoach: involves adapting an existing model to the system of interest which incorporates as detailed a description of that system as the art of ecological theory allows.
Black-box/white-box approaches (Beck 1981; Jorgensen 1986)	Black-box approach: involves constructing a model designed solely as a quantitative description of how a change in input variables affects the output of the system.
	White-box approach: involves constructing a model which deals explicitly with the causal relations linking system inputs, internal system states and system outputs.
Holistic/reductionist approaches (Jorgensen 1986)	Holistic approach: involves constructing a model which explicitly includes properties of the system working as an integrated unit.
	Reductionist approach: involves constructing a model which incorporates as many details of the system as possible, in order to fully capture its behavior.
External/internal approaches (Rosen 1969; Kerr 1982)	External approach: involves observing (describing) some integral behavior of the system of interest and then proceeding to understand how that behavior is brought about.
	Internal approach: involves assembling known behavior of individual subsystems, in order to reveal something useful about the overall behavior of the system of interest.
Empirical/analytical approaches (Rigler 1982)	Empirical approach: involves constucting a model whose sole function is to predict future states of the system of interest.
	Analytical approach: involves constructing a model which predicts future states but, in addition, embodies a detailed explanation of why the system of interest behaves as it does.

selectivity. A major change in the age selectivity of the fishing gear will bring a different segment of the stock under exploitation and this can produce significant and inherently unpredictable changes in the constants of the surplus production model (Fig. 1). These changes are inherently unpredictable because the simple surplus production model does not explicitly describe how potential yield is determined by the interaction between gear selectivity and size structure: this process is merely summarized in the values of two or three empirically derived constants. However, the effects of changes in gear selectivity can be evaluated by using a model which explicitly includes age structure effects: just such a model was used to derive the curves in Fig. 1. Expanding the situation further, age structured models alone become inadequate if we wish to forecast when gear changes will occur, as well as their consequences. An attack on this problem would require a larger model, incorporating the economic forces driving the fishing industry itself. Further expansions in any direction quickly lead to overblown constructs that deal explicitly (and inadequately) with processes operating on a global scale.

This example illustrates the fact that model expansion does not eliminate the SA: it merely limits its application to processes which are somewhat removed from those of immediate interest. The cost of this distancing is a rapid increase in the complexity of the forecast

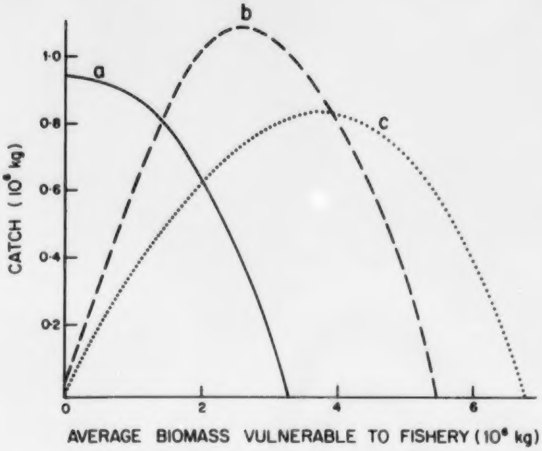


FIG. 1. Relations between sustainable catch (=net production) and fishable biomass estimated for different segments of the Lake Erie walleye population using the age-structured model of Shuter and Koonce (1977). Segments are (a) all ages >7; (b) all ages >3; (c) all ages >1.

model. When developing an explanatory model for forecasting, a primary objective should be to obtain a reasonable amount of distancing without generating a very complex model. Very complex models are not often successful in generating useful forecasts (Brewer1986).

Similar problems are associated with the use of empirical models. Demands for increased precision can be met by adding more independent variables to the regression equation, but there is no formal way of reinforcing the credibility of the SA . The constants in a valid empirical model summarize the responsiveness of a system to changes in environmental variables during the historical period when the data were collected. The approach provides no information on whether/how these values might change in the future. The fact that a "good" empirical relation can be derived from historical/comparative data implies that the derived relation has been stable in the past. This alone lends some credibility to the hypothesis that it will remain stable for some period into the future. However, as the forecast horizon recedes, the credibility of this version of the SA will also decline. As Brewer (1986) points out, the future is not encompassed by the past: the older the data used and/or the farther into the future analyses are pushed, the more likely are surprises.

Recently, both Rigler (1982) and Walters (1987) have criticized classical population dynamics modeling on the grounds that the credibility of the SA declines too rapidly for such models to generate useful forecasts. While both authors agree on this fundamental point, the conclusions they draw from it are very different. Rigler recommends that stock-based models be abandoned. Walters suggests that their use be modified to both detect and correct changes in parameter values. This has the effect of altering the basic character of an SA forecast: the tentative nature of its predictive role is explicitly recognized plus it is give a new role as a benchmark for detecting the unexpected. The utility of this approach is illustrated in Walters (1987) and Shuter et al. (1985) (Fig. 2).

The criticisms of Rigler and Walters cannot be rejected in principle, but they can be tested in practice. Walters (1987) examined time series data from several stocks and found examples of both stable and unstable empirical production models. In our work with walleye and smallmouth bass (Fig. 3), we have found that some parameters of the stock-recruit relation can remain relatively stable for decades. In addition, many of the primary parameters involved in processes linked directly to biomass production are strongly limited with respect to the values that they can assume. For example, bioenergetic parameters (e.g. basal and maximum metabolic rate, minimum swimming cost) in analytical models are constrained by the size of the animal and by

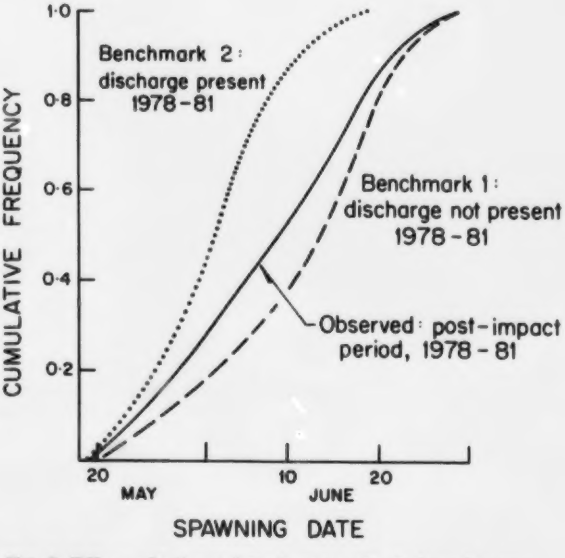
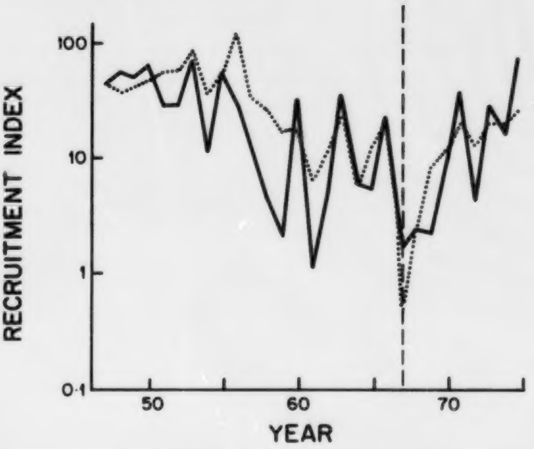


FIG. 2. Effects of a thermal discharge on the timing of spawning in Baie du Dore smallmouth bass: comparison of benchmark forecasts of potential effects with observed post-impact behavior (after Shuter et al. 1985). The cumulative frequency distribution of observed spawning dates for the years 1978–81 falls between the distributions generated by two benchmark forecasts. The first benchmark is a forecast of the expected distribution of spawning dates with the thermal plume absent. The second benchmark forecasts the distribution expected with the plume present. Since the observed distribution falls between the two benchmarks, we conclude that the forecast model captures the basic character of the thermal plume's effect on the timing of spawning, but overestimates its intensity.

a. Lake Erie Walleye



b. Lake Opeongo Smallmouth Bass

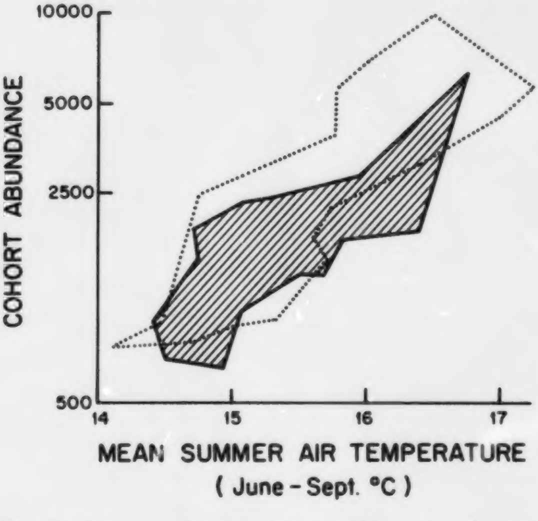


FIG. 3. Two examples of relative stability of production parameters over extended periods of time. (a) Lake Erie Walleye (from Shuter and Koonce 1977): the stock–recruit relation derived from 1948 to 1967 data (vertical dashed line marks 1967) is sufficient to account for stock behavior over the period 1968–76. (b) Lake Opeongo Smallmouth Bass (Shuter, unpubl. data): the 1937–56 regression relation linking adult cohort strength to weather conditions during early life (hatched area shows data distribution) is statistically indistinguishable from the same relation for period 1957–76 (dotted line outlines data distribution).

a variety of physical processes (e.g. turbulence, O_2 and nutrient diffusion: Munk and Riley 1948; Hurlburt 1970; Peters 1983). Population level parameters (e.g. intrinsic rate of increase, natural mortality rate) are also constrained by body size, broad taxonomic groupings and environmental conditions (Beverton and Holt 1959; Southwood 1976; Peters 1983; Pauly 1980). These empirical results suggest that changes in some of the important parameters of stock-based production models are likely to be slow and relatively limited.

We draw the following tentative conclusions from the findings presented above:

1) Reliable, short to medium-term (days to years) forecasts that focus on predicting direction and bounds of change at the stock level can be constructed for many real situations.
2) Short-term forecasts that predict the absolute magnitude of change play two roles. First, they serve as best estimates of expected change, given current knowledge of the system. Second, they serve as devices for early detection and interpretation of unexpected behavior in the system: by explicitly stating what is expected, they permit ignorance (the unexpected) to be recognized and corrected. Both roles are of value since real situations cover the full range, from stable to stochastic. Full development of both roles can only occur in the ideal situation where there is ongoing monitoring of both the population and its environment, coupled with iterative reassessment of the impact of any environmental changes on the population (Beanlands and Duinker 1983; Ravetz 1986). In most situations, emphasis on the second role should increase with the length of the forecast.

The Analytical Approach to Forecasting

The analytical approach to forecasting changes in population abundance can be split into two stages. The first involves estimating the immediate effects of environmental changes on typical population members. The second involves evaluating the ultimate effects of such changes on average adult abundance. Immediate effects are expressed as changes in the original age-specific rates of mortality, growth and reproduction. The forecast horizon is short (usually less than the generation time of the target organism) and the problem is often tractable, even in the generally complex case of mobile organisms confronted with localized environmental changes (Shuter et al. 1985).

The focus on mortality and reproductive rates is unavoidable since both are required for any forecast of population numbers. In fisheries, the additional focus on individual growth rates stems from the fact that age specific growth rates in fish are flexible and their variation can lead directly to changes in survival and fecundity. Some examples of the analytical approach to forecasting are summarized in Table 2.

Central to each example is a quantitative description of how a typical individual responds to a change in its

TABLE 2. Examples of the analytical approach to modeling and forecasting.

Focus of study	Definition of problem	Internal and external constraints on individuals	Potential applications
Algae: environmentally induced changes in cell composition (Shuter 1979; Laws et al. 1983).	Organism relocates cell carbon amongst essential parts to maximize growth.	Efficiencies of protein synthesis, photosynthesis and nutrient uptake are fixed; maintenance metabolism depends on size of individual and temperature.	Forecast effects on population growth of changes in light, nutrient levels and temperatue (Schlesinger et al. 1981).
Fish: response of predator activity and growth to changes in pey size, prey availability and temperature (Ware 1978; Crowder and Magnuson 1982).	Organism adjusts activity to maximize net energy gain.	Maintenance metabolism, maximum metabolism and foraging costs depend on size of individual and temperature	Forecast effects on predator growth and prey mortality of changes in prey size, predator abundance and temperature (Ware 1978; Kitchell and Beck 1980).
Fish: ontogenetic changes in utilization of different habitats (Werner and Gilliam 1984).	Organism allocates amount of time spent in different habitats to maximize lifetime production of offspring.	Growth rate and vulnerability to predation depend on the size of the individual and the habitat it occupies.	Forecast effects on growth and mortality of changes in the availability of different habitats.
Fish: changes in spatial distribution in response to local changes in temperature (Coutant and Carrol 1980).	Organism selects temperature which maximizes its scope for growth.	Scope for growth rises and falls with increasing temperature.	Forecast how spatial distribution of fish changes with changes in local temperatures (Coutant 1985, 1987).
Fish: changes in recruitment in response to local changes in temperature (Shuter et al 1980).	Adult organism adjusts timing of spawning to minimize mortality of offspring.	Larval mortality increases if spawning occurs too early; winter mortality increases if spawning occurs too late.	Forecast effects on recruitment variation of local changes in temperature (Shuter et al. 1985).

environment. Estimating likely exposure to change is the first step in such a description (The Exposure Problem). The spatial distribution of the environmental change and the mobility of the organisms affected are of primary importance in determining how to deal with the exposure problem (Fig. 4). The most difficult situation to deal with involves mobile animals faced with localized environmental changes. Movement of these organisms in response to the spatial distribution of new environmental conditions must be considered when calculating the average exposure of a typical individual (Fig. 5). In a sense, a second level of biological response must be added to the problem: the movement of individuals relative to the impacted area must be forecast as well as the response of the typical individual to the average change it experiences.

The examples cited (Table 2) deal with pervasive and localized changes. In each example, model construction begins by specifying sets of constraints which act both to restrict the potential response of the animal to change and to determine the consequences (i.e. effects on growth, mortality or reproduction) of whatever response is elicited by the change. These constraints are the biological and environmental "givens" of the situation. The response itself can often be cast in terms of an allocation or timing problem: in energetics models

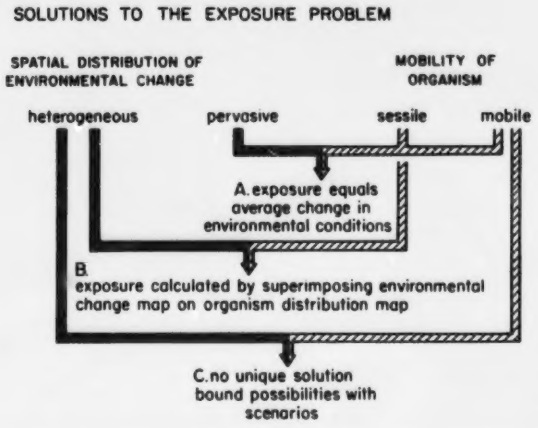

SOLUTIONS TO THE EXPOSURE PROBLEM
SPATIAL DISTRIBUTION OF ENVIRONMENTAL CHANGE
MOBILITY OF ORGANISM
heterogeneous
pervasive
sessile
mobile
A. exposure equals average change in environmental conditions
B. exposure calculated by superimposing environmental change map on organism distribution map
C. no unique solution bound possibilities with scenarios

FIG. 4. Solutions to the Exposure Problem: how to estimate the average exposure of a typical population member to a change in environmental conditions. Solutions fall into three broad categories depending on the spatial distribution of the change and the mobility of the organism. Categories A and B require little more than superimposing a map of the spatial distribution of changes onto a map of the spatial distribution of organisms. Category C is more complex: here the organism can react to the spatial distribution of changes by redistributing itself. Bounds on exposure can be estimated by using a series of well-defined scenarios to explore the range of possible redistributions.

(Ware 1978), how should available energy be allocated among prey search, somatic growth and production of reproductive products? In the smallmouth bass model, and some insect models (Gilbert et al. 1976), how should timing of reproduction be synchronized to the annual cycle of temperature and resource availability? Specification of all obvious constraints is usually not sufficient to determine a particular response, rather it delineates a range of feasible responses along with their consequences. This range of consequences can be bounded in a meaningful way using three bench mark scenarios:

1) Adaptive/best case scenario — the response elicited by the environmental change is one which maximizes some correlate of fitness (e.g. fish: allocation of energy to foraging is such that net energy gain is maximized: Ware 1978; algae: allocation of carbon to chloroplasts and ribosomes is such that cell doubling time is minimized: Shuter 1979);
2) No response/null scenario — no specific response is elicited by the environmental change; the animal is indifferent to the change and suffers the consequences of that indifference (e.g. when lamprey were introduced to the Great Lakes, the resident lake trout had no defences in place to deal with this unfamiliar predator and thus suffered a large increase in mortality: Smith and Tibbles 1980);
3) Maladaptive/worst case scenario — the response elicited is one which unnecessarily reduces some correlate of fitness (e.g. adult smallmouth bass were attracted to the thermal plume of the Baie du Dore power plant; the resulting concentration of fish increased angler catchability and thus increased bass mortality: Shuter et al. 1985).

A concrete illustration of this approach to bounding the exposure problem is given in Fig. 5.

In many situations, the "familiarity" of the expected environmental change can be used to assess the likelihood of each of the three benchmark scenarios. A "familiar" change involves an environmental component which varies naturally and whose range of variation is not greatly affected by the change. (e.g. moderate alteration of annual temperature regime produced by power plant thermal plume). In these circumstances, it is likely that the organism will respond actively to compensate for (or take advantage of) changes in the environmental factor concerned. Therefore, we would expect the observed response to be close to the best case scenario. The kind of reasoning used to construct adaptive scenarios borrows explicitly from the optimization school of academic ecology and shares all the strengths and weaknesses of that approach (Oster and Wilson 1978).

An "unfamiliar" change involves an environmental component that does not vary naturally (e.g. heavy metals, exotic toxic materials). Since there is no reason to expect that the animal would be capable of actively responding to the change at all, we would anticipate the observed response to be closest to the null scenario.

Finally, a "familiar change in an unfamiliar context" can involve a very large shift in a naturally varying variable (e.g. creation by a thermal plume of warm areas lasting through winter). It can also involve the creation of a linkage between a familiar variable and an unfamiliar one (e.g. placing a trap net at the offshore end of an artificial obstruction — the net lead). Independent of the exact mechanism, the overall effect is that the animal responds to the changed environment by doing "the wrong thing for the right reason": an unfamiliar context turns what would have been an ameliorative response (seeking deep water to avoid beaching, seeking warm water to increase scope for growth) into a maladaptive one (see also Fig. 5). Under these circumstances, we would expect the observed response to be closest to the worst case scenario.

Once immediate effects on existing individuals have been evaluated, the ultimate effects on average adult abundance must be determined. Experience with exploited populations has shown that additional mortality among adults leads to a decline in adult abundance

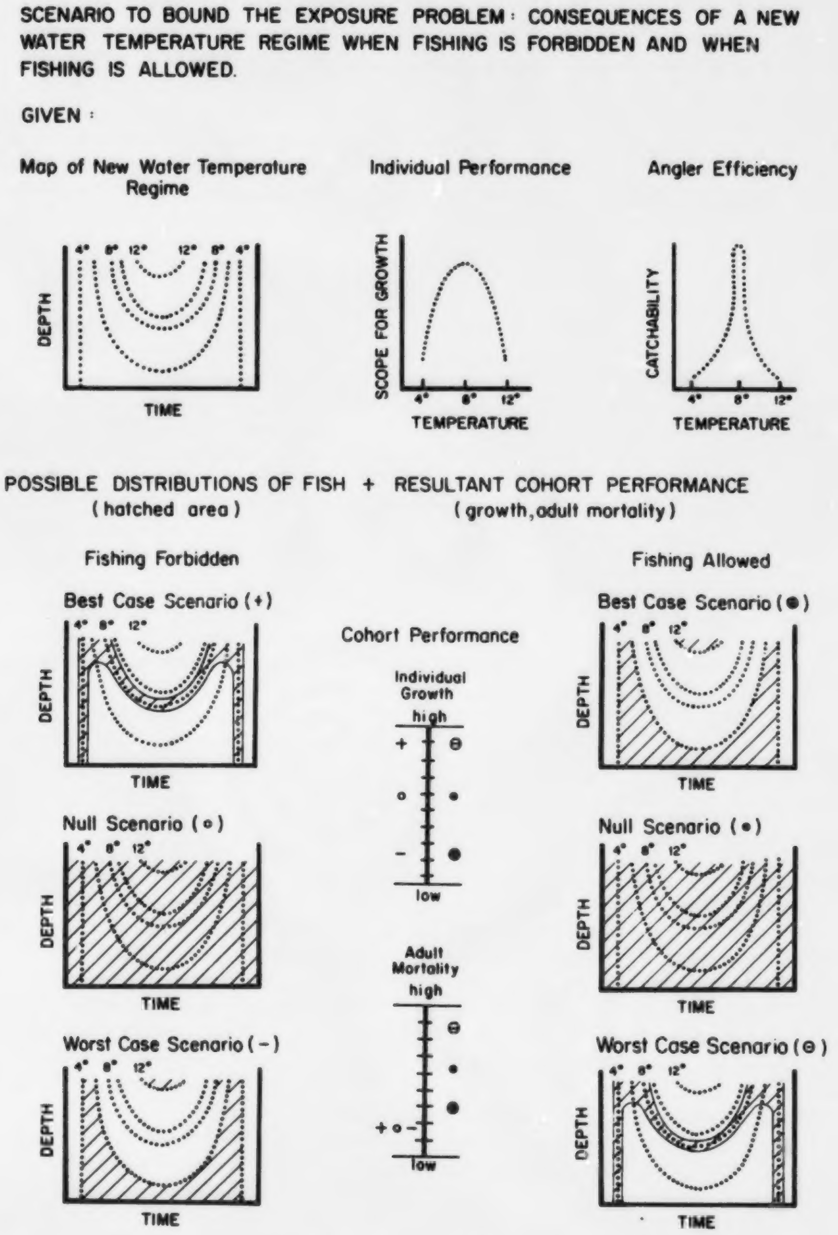

SCENARIO TO BOUND THE EXPOSURE PROBLEM: CONSEQUENCES OF A NEW WATER TEMPERATURE REGIME WHEN FISHING IS FORBIDDEN AND WHEN FISHING IS ALLOWED.
GIVEN:
Map of New Water Temperature Regime
Individual Performance
Angler Efficiency
4° 8° 12° 12° 8° 4°
DEPTH
TIME
SCOPE FOR GROWTH
4° 8° 12°
TEMPERATURE
CATCHABILITY
4° 8° 12°
TEMPERATURE
POSSIBLE DISTRIBUTIONS OF FISH + RESULTANT COHORT PERFORMANCE
(hatched area)
(growth, adult mortality)
Fishing Forbidden
Fishing Allowed
Best Case Scenario (+)
4° 8° 12°
DEPTH
TIME
Cohort Performance
Individual Growth
high
+
ʘ
o
•
–
●
low
Best Case Scenario (●)
4° 8° 12°
DEPTH
TIME
Null Scenario (o)
4° 8° 12°
DEPTH
TIME
Adult Mortality
high
ʘ
•
●
+ o –
low
Null Scenario (•)
4° 8° 12°
DEPTH
TIME
Worst Case Scenario (–)
4° 8° 12°
DEPTH
TIME
Worst Case Scenario (ʘ)
4° 8° 12°
DEPTH
TIME

FIG. 5. Use of scenarios to bound the potential effects on cohort performance of a change in the spatial/temporal distribution of water temperatures. The upper set of figures defines the situation: the new water temperature distribution plus the effects of temperature on fish performance and angler efficiency. The lower sets of figures give the forecasts of fish distribution and cohort performance under best, null and worst case scenarios when fishing is forbidden and when it is allowed. Each scenario is described by the distribution of fish it generates and the consequences of that distribution for cohort performance, as measured by individual growth and adult mortality. Since mortality is given a higher weight than growth when evaluating the overall consequences of each scenario, adding fishing to the initial set of scenarios transforms best case to worst, and vice versa.

that is often predictable from classical population dynamics models (e.g. Shuter et al. 1987). The components of natural mortality among adults remain largely unaffected by the imposition of new sources of mortality or the intensification of old sources. However, during early life the components of natural mortality appear to be quite flexible. Higher mortality from one source causes density to decline and this, in turn, causes a reduction in mortality from other sources. As a result, adult abundance is strongly buffered against changes in the vital parameters (mortality and growth rates) of younger age groups. Experience with exploited populations (Parrish 1973) has shown that most natural stocks have some buffering capacity (e.g. some scope to compensate for additional mortality in early life history stages), but this has proved very difficult to measure. In impact assessment situations, this difficulty has been circumvented by applying variants of the following argument:

a) Assume compensatory scope equals zero for the earliest life history stage affected, and for all succeeding stages;
b) Forecast immediate changes in vital parameters for all affected life stages;
c) Evaluate the accumulated effects of all these changes on the adult abundance of a typical cohort (Ricker 1975, chap. 10);
d) Assume these changes in adult abundance do not affect the rate at which juvenile fish recruit to the adult segment of the population.

In the final Hudson River striped bass assessment, parts (a) through (c) were used (Barnthouse et al. 1984). It was explicitly recognized that (a) was a worst case assumption, but this was deemed acceptable given the absence of reliable scientific knowledge on compensation in the Hudson River population. In the Baie du Dore smallmouth bass assessment (Shuter et al. 1985), parts (a) through (d) were justified empirically. Statistical analysis of historical data on adult abundance showed that, prior to impact:

1) the adult abundance of an individual cohort was strongly dependent on the environmental conditions existing immediately after that cohort was spawned; this indicates little compensatory scope after fertilization and, therefore, justifies assumption (a) above;
2) wide variation in the number of spawning adults had little effect on the adult abundance of individual cohorts; this indicates strong compensatory scope prior to fertilization and justifies assumption (d) above.

As outlined above, usable solutions to both the exposure problem and the adult abundance problem can be obtained by estimating realistic bounds for abundance changes rather than trying to predict exactly what those changes will be. Typically this is done through a small set of carefully constructed scenarios which explicitly set out to caricature reality along "best case" and "worst case" lines. Extreme scenarios like these are often easier to deal with objectively than those that try to capture reality as it is. Because they do not purport to contain everything that may be important in determining short-term fluctuations in abundance, they are less subject to charges of incompleteness. In contentious situations, they serve to channel debate along constructive lines and can form the basis for regulatory decisions (e.g. Hudson River striped bass).

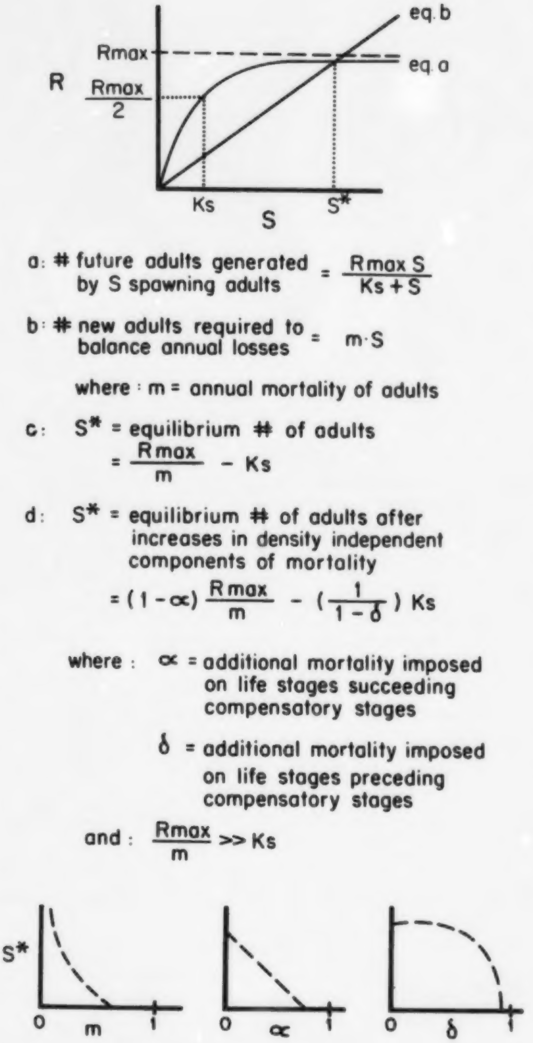
Our discussion so far has been shaped primarily by the role compensation has played in complicating power plant impact assessment. This is a special case, because many such assessments assume that the only impact involved amounts to the imposition of an additional, density independent component of mortality on some segment of the affected fish population. The wider problem of dealing with habitat change in general demands some strategy which could handle changes in both the density dependent as well as the density independent components of mortality. Before getting into this issue, it will be helpful to look at compensation again in a more formal way.

The influence of compensatory effects on the stability of adult abundance is summarized in Fig. 6. This scheme is based on the following assumptions:

1) The compensatory scope for most populations is largely a property of a critical set of early life history stages (McFadden 1977; Beverton 1984).
2) In most situations, the nature of the compensatory effects are such that the relationship, between number of breeding adults and number of young that survive to breed, follows a saturation curve (Shepherd 1982; Solomon 1985).

Figure 6 is our attempt at a simplified expression of the primary notions which embue current literature on compensation (Chen 1987).

Equilibrium analyses (Fig. 6) indicate that additional mortality can affect average adult abundance in a variety of ways. If initial adult abundance is high, then a moderate increase in mortality will have little effect, provided that it is imposed on a life-stage which precedes those primarily responsible for the compensatory scope of the population. Adult abundance will vary directly with additional mortality, if it is imposed on life-stages which follow the compensatory stages. If initial adult abundance is low, any additional mortality will produce a corresponding reduction in the rate of population growth: under these circumstances, compensatory effects are no longer important. The argument of Fig. 6 applies only to those changes in habitat which elevate the density independent components of mortality (e.g. impingement by power plants, moderate reductions in pH due to acid rain) on some segment of the target population. Habitat changes which produce a decrease in the amount of living space or food available to members of the target population may produce



a: # future adults generated by S spawning adults $= \dfrac{R\max S}{Ks+S}$

b: # new adults required to balance annual losses $= m \cdot S$

where : m = annual mortality of adults

c: S^* = equilibrium # of adults
$= \dfrac{R\max}{m} - Ks$

d: S^* = equilibrium # of adults after increases in density independent components of mortality
$= (1-\alpha)\dfrac{R\max}{m} - \left(\dfrac{1}{1-\delta}\right) Ks$

where : α = additional mortality imposed on life stages succeeding compensatory stages

δ = additional mortality imposed on life stages preceding compensatory stages

and : $\dfrac{R\max}{m} >> Ks$

FIG. 6. A simple description of compensation in a fish population. The upper figure and equation (a) illustrate how the number of new individuals (R) entering the adult segment (S) of the population depends on S: a typical stock–recruit relation. Equation (b) gives the rate at which individuals are lost from the adult segment of the population. Equation (c) gives the equilbrium size (S*) of the adult segment of the population. Equation (d) shows how S* is affected by increasing density independent mortality for different stages of the life cycle. These effects are illustrated in the lower three figures.

a decrease in $R_{\max}$ and a consequent decrease in adult population abundance according to the formula:

$$S^* = \frac{R_{\max}}{m} - K_s$$

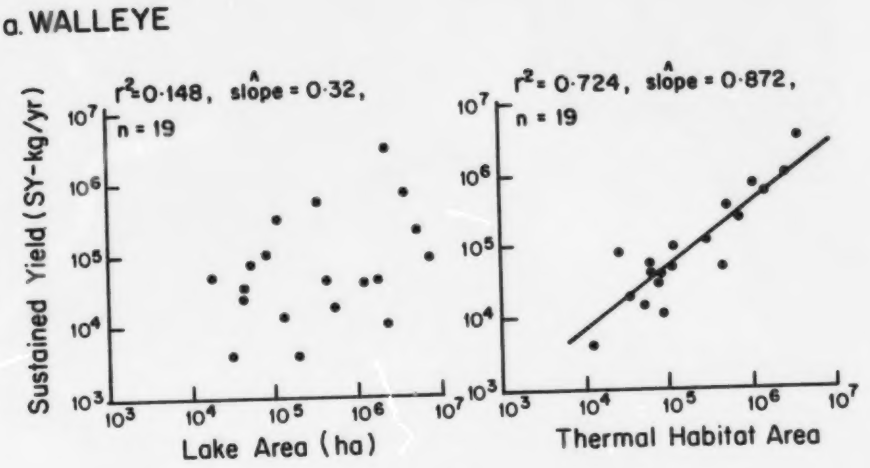
Reisenbichler (1989) provides an interesting example of this kind of effect. Christie and Regier (1988) provide a broad empirical demonstration (Fig. 7).

Christie and Regier showed that population production for some species is essentially proportional to the amount of usable space available to the population. They used analytical work on the temperature preferences of individuals plus detailed 3 dimensional maps of lake temperatures to calculate the amount of thermally optimal space (area for the littoral walleye, volume for the pelagic lake trout) available for a given species in a number of lakes. Regression analysis showed that this refined measure of available living space provided a more precise measure of population production than simple lake area. Their work provides one example of how empirical analysis can be used to apply knowledge about individual organisms to the study of population level phenomenon. Empirical analysis can also be used to introduce knowledge of population-level phenomena into analytical studies of individuals. Stock-recruit analysis plays this role when it is used to define the levels of adult abundance where compensatory effects become important (Shepherd 1982) or to isolate those life history stages where such effects are expressed (Elliot 1985).

In the examples cited above, one (Christie and Regier 1988) shows how knowledge derived from analytical studies of individuals can be used to refine independent variables used in an empirical study of populations. In the others (Shepherd 1982; Elliot 1985), empirical relations developed at the population level show how to model compensation analytically, by imposing separate constraints on the mortality rates assigned to each stage in the life history of the organism. These examples illustrate how the empirical and analytical approaches can be used to produce composite models which embody knowledge from several organizational levels into a single, logically consistent structure. We will return to this theme in later sections of the paper.

The Empirical Approach to Forecasting

The empirical approach to forecasting is based on statistical associations which link population-level variables (abundance, production, natural mortality) to population abundance and/or selected environmental variables. There are two versions of this approach: historical and comparative. Historical analysis generates a forecasting model which is specific to a particular stock. Typically, multiple regression of time series data from the stock of interest produces a model which will forecast future abundance, given present abundance and future environmental conditions. Comparative analysis generates a predictive model which can be applied to many different stocks. Typically, multiple regression of population and environmental data from a sample of stocks produces a model which can be



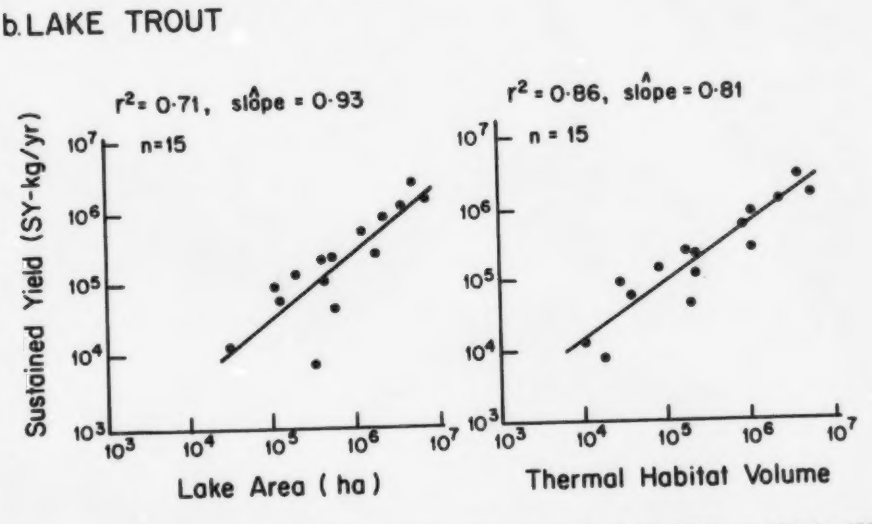


FIG. 7. Comparative analysis of sustained yield in walleye and lake trout stocks (after Christie and Regier 1988). Log-log linear regression results are presented above each graph. (a) Walleye: Sustained yield versus lake area and thermal habitat area for 19 separate lake populations. Thermal habitat area is a time integrated measure of the bottom area of the lake that experiences temperatures within 2°C of the optimal growth temperature for walleye (units: hectares per 10 days). Area was chosen because the walleye is a bottom oriented, littoral predator. The correlation between sustained yield and thermal habitat area is significantly ($P<0.05$) higher than that between sustained yield and lake area. The slope of the thermal habitat regression equation is not significantly ($P>0.05$) different from 1.0: thus, sustained yield is proportional to thermal habitat area. (b) Lake trout: Sustained yield versus lake area and thermal habitat volume for 15 separate lake populations. Thermal habitat volume is a time integrated measure of the volume of the lake that experiences temperatures within 2°C of the optimal growth temperature for lake trout (units: cubic hectometres per 10 days). Volume was chosen because the lake trout is a pelagic predator. The correlation between sustained yield and thermal habitat volume is higher than that between sustained yield and lake area. The slope of the thermal habitat regression equation is not significantly($P>0.05$) different from 1.0: thus, sustained yield is proportional to thermal habitat volume.

applied to any similar stock. Such models are usually designed to predict hard-to-measure population variables (e.g. natural mortality rate: Pauly 1980; production: Christie and Regier 1988; abundance: Milner et al. 1985) from easily measured population and environmental variables.

The primary shortcoming of the empirical approach lies in the fact that it is purely descriptive. Since no cause/effect structure is embedded in an empirical model, it can only generate reliable forecasts in situations similar to those reflected in the data used to construct it: empirical methods are not reliable in unfamiliar situations. The main limitations of both historical and comparative analyses are summarized in Table 3.

TABLE 3. Limitations of the empirical approach to modeling population behavior.

Historical analyses	Comparative analysis
The derived model may be based on a spurious correlation.	The derived model may be based on a spurious correlation.
A long time series of data must be established before the approach may be applied: in some cases, the system may be changing on a time scale shorter than that necessary to describe it.	A model derived from a comparison of different systems may contain relations that differ greatly from those that govern the dynamics of one specific system.
The predictive value of such models has rarely been described using data independent of that used to build the model.	
The data required can be so "noisy" that a useful description of the compensatory scope of the population cannot be obtained.	

Two recently published comparative analyses (Christie and Regier 1988, Goddard et al. 1987) illustrate the potential role of organism and community level knowledge in such studies. Christie and Regier (1988) showed that equilibrium yields from limnetic sport fish populations were strongly correlated (Fig. 7) with the amount of thermally optimal habitat available over a typical growing season. They used information on the performance characteristics of individual organisms (optimal growth temperatures) to filter raw environmental information and produce a composite variable carefully designed to capture the interaction between environment and individual. The results reported by Christie and Regier show that such composite variables can significantly improve the precision and accuracy of comparative models.

The study by Goddard et al. (1987) is interesting because it demonstrates one use of community level information in comparative studies. Goddard et al. studied the associations between lake area, lake trout harvest and sport fishing effort in a sample of Ontario lakes. A fish species list was available for each lake, as well as information on lake trout diet, so that the data set could be subdivided in a variety of ways and the harvest/effort and effort/area associations compared across subdivisions. For example, populations in lakes containing lake trout competitors (e.g. whitefish, burbot) were compared to populations with no competitors and piscivorous lake trout populations were compared to strict plankton feeding lake trout populations. Subdividing the data set by community type significantly improved the precision of the effort/lake area model (Fig. 8): populations lacking competitors could withstand higher effort levels than those with competitors. In general, such splitting procedures should provide more precise models of situations where there are strong community-based constraints on population abundance.

The roles of different kinds of information in empirical studies of population behavior can be summarized as follows. Consider the simple analysis of covariance model as typical of the products of such studies:

$$
\begin{aligned}
Y &= a_1 + b_1 X, \text{ for stocks of type 1}\\
Y &= a_2 + b_2 X, \text{ for stocks of type 2}\\
&\vdots \qquad\quad \vdots\\
Y &= a_n + b_n X, \text{ for stocks of type } n
\end{aligned}
$$

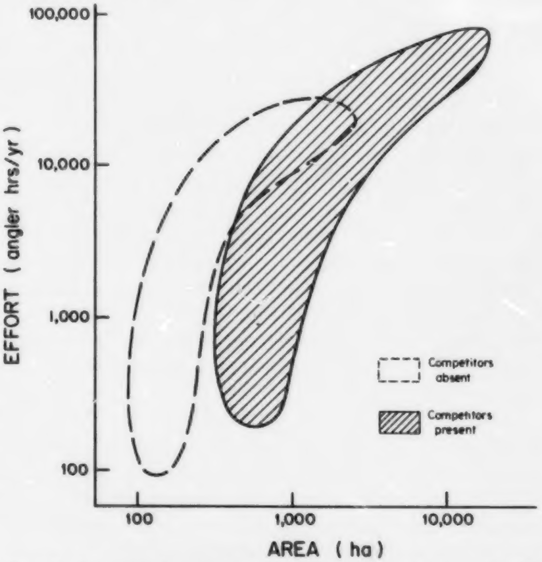


FIG. 8. Comparative analysis of effort/area relations for 87 Ontario lake trout stocks (after Goddard et al. 1987).

Knowledge of the structure, function and life history of the populations of interest is used to select a useful dependent variable (*Y*, e.g. production, mortality rate). Knowledge of interactions between relevant abiotic/biotic factors and individual stock members is used to construct a meaningful independent variable (*X*, e.g. optimal thermal habitat area). Knowledge of differences in the community context experienced by different stocks permits the data set to be split into n subdivisions: the effect of community context on the association between *Y* and *X* is evaluated by quantitative comparisons of that association across subdivisions. This scheme provides a formal illustration of the ways in which information from organizational levels above (community) and below (organism) the level of interest (population) can be integrated into a single empirical study.

Synthesis

The empirical approach is used to identify and describe pattern at the population level (e.g. associations among recruitment, adult abundance and environmental factors). The analytical approach is used to define a sufficient explanation for that pattern and to elaborate the explanation in terms of the cause/effect relations that govern the behavior of individual population members.

A pure empirical approach suffers from its inability to distinguish between pattern based on causal relations among variables, and pattern based on casual associations. A pure analytical approach suffers from its inability to identify those aspects of individual behavior that are likely to exert a strong influence on population behavior.

Since the strengths and weaknesses of the two approaches compliment each other, explicit use of both should lead to more effective forecasting tools. Analytical work on individuals can provide more effective independent variables for empirical studies of pattern at the population and community levels (e.g. Christie and Regier 1988). This use of autecological knowledge to filter raw environmental measurements should provide sets of independent variables that are less likely to produce spurious correlations. Similarly, analytical models can be made more comprehensive by introducing parameter constraints derived from empirical descriptions of population and community level properties.

Thus, by linking both the empirical and analytical approaches, we can generate composite population models which embody knowledge from several levels of organization into a single, logically consistent structure. We found such a composite model of real use in a power plant impact assessment (Fig. 9). Van Winkle et al. (1986) have proposed such a composite model be developed as a forecasting tool for acid rain impact

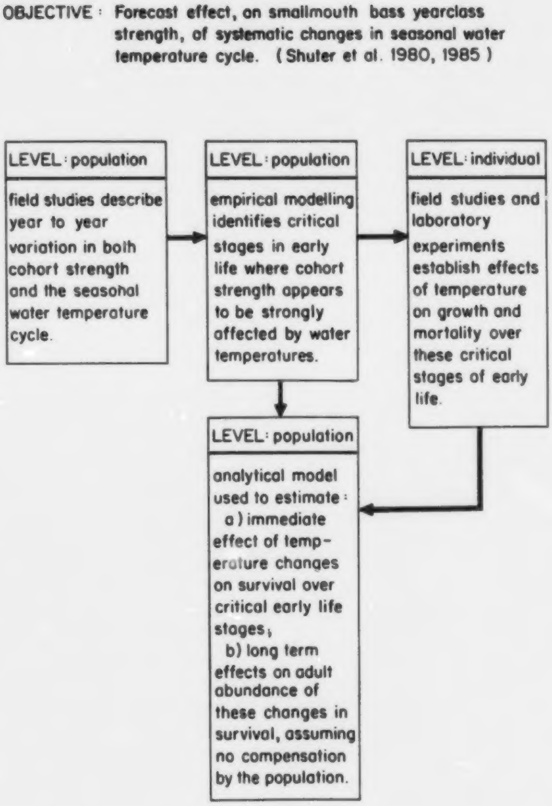

OBJECTIVE: Forecast effect, on smallmouth bass yearclass strength, of systematic changes in seasonal water temperature cycle. (Shuter et al. 1980, 1985)
LEVEL: population
field studies describe year to year variation in both cohort strength and the seasonal water temperature cycle.
LEVEL: population
empirical modelling identifies critical stages in early life where cohort strength appears to be strongly affected by water temperatures.
LEVEL: individual
field studies and laboratory experiments establish effects of temperature on growth and mortality over these critical stages of early life.
LEVEL: population
analytical model used to estimate:
a) immediate effect of temperature changes on survival over critical early life stages;
b) long term effects on adult abundance of these changes in survival, assuming no compensation by the population.

Fig. 9. Steps involved in assessing the impact of power plant development on the Baie du Dore smallmouth bass population (Shuter et al. 1985).

Data were collected at both the population and individual levels. Field studies at the population level established that adult cohort strength varied widely from year to year. Field studies at the individual level established that: the survival of larvae in individual nests varied widely with water temperature and that larval developmental rate and fry growth rate were also strongly dependent on temperature. Laboratory studies at the individual level documented the temperature dependence of growth, winter starvation and survival.

Data analysis used both empirical and analytical methods. Empirical studies established that adult cohort strength was strongly correlated with weather conditions experienced during early life. An analytical model of the first year of life was built from the relations linking water temperature to nest success, fry growth and winter survival. The model showed that these processes were sufficient to explain the observed variation in cohort strength. The model was then used to forecast the long term impact of power plant development, assuming fixed initial cohort size and no compensation.

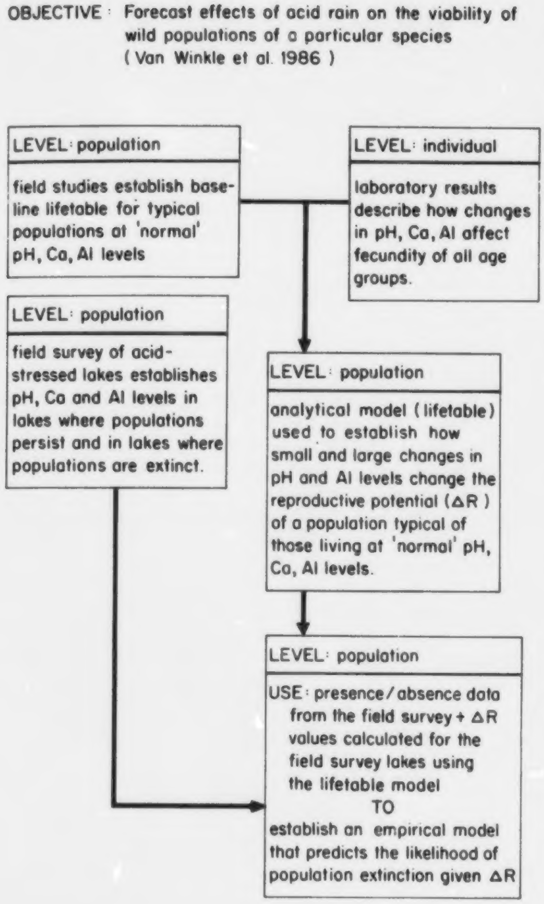

OBJECTIVE : Forecast effects of acid rain on the viability of wild populations of a particular species (Van Winkle et al. 1986)
LEVEL: population
field studies establish baseline lifetable for typical populations at 'normal' pH, Ca, Al levels
LEVEL: individual
laboratory results describe how changes in pH, Ca, Al affect fecundity of all age groups.
LEVEL: population
field survey of acid-stressed lakes establishes pH, Ca and Al levels in lakes where populations persist and in lakes where populations are extinct.
LEVEL: population
analytical model (lifetable) used to establish how small and large changes in pH and Al levels change the reproductive potential (ΔR) of a population typical of those living at 'normal' pH, Ca, Al levels.
LEVEL: population
USE: presence/absence data from the field survey + ΔR values calculated for the field survey lakes using the lifetable model
TO
establish an empirical model that predicts the likelihood of population extinction given ΔR

FIG. 10. Study plan to develop a method for forecasting the acid rain tolerance of wild fish stocks (Van Winkle et al. 1986).

Data are to be collected at both the individual and population levels. Empirical studies at the population level establish "normal" life tables for unstressed stocks. Empirical studies at the population level establish changes in pH and Al concentrations at a series of carefully chosen sites representative of the following situations: native stock stable in the face of pH/Al stress; native stock extinct due to pH/Al stress. Laboratory studies on individuals document how pH/Al stress affects life table parameters (mortality and fecundity rates).

Data analysis will employ both analytical and empirical methods. The laboratory toxicity results and a life table model, calibrated to the data on unstressed stocks, are used to estimate decreases in reproductive potential (ΔR) produced by exposure to the pH levels and Al concentrations found at the sites of stable and extinct stocks. These ΔR values are then used to estabish an empirical relation between ΔR and likelihood of extinction. This last relation is the final objective of the study: a tool for estimating the probability of stock extinction from the pH and Al levels that the fish experience.

assessment studies (Fig. 10). Holtby and Scrivener (1989) have shown that such composite models can be useful in assessing the impact of habitat change. We believe that such composite models provide an effective solution to the problem of generating credible population forecasts when there are strong interactions between different levels of biological organization. They should be of real value in quantifying how changes in fish habitat affect population abundance.

Acknowledgments

Useful comment and ideas were provided by D. Evans, B. Henderson, C. Levings, J. MacLean, P. MacNamee and several anonymous reviewers. A. Chui drafted the figures.

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The Puget Sound Runs of Salmon: An Examination of the Changes in Run Size since 1896[1]

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Abstract

BLEDSOE, L. J., D. A. SOMERTON, AND C. M. LYNDE. 1989. The Puget Sound runs of salmon: an examination of the changes in run size since 1896, p. 50–61. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

With the development during this century of the Puget Sound region of Washington State, USA, came changes to many factors having a potential impact on the productivity of wild salmon runs. This study estimates indices of the annual sizes of these runs over as long a period as data allow and attempts to determine whether the runs have changed with time. Since the available data do not extend backwards to the same point in time for all species and areas, the period from 1896 to 1975 has been broken into three shorter intervals. For each period one or more methods to estimate indices of run size have been used. Regression techniques are used to detect any time trends in run indices. The analysis was unable to indicate with statistical confidence that the wild run of chinook and coho salmon to all of Puget Sound was substantially different between 1975 and 1896, however, runs to specific areas within the Sound probably have decreased. Wild run estimates over a 10-year period contained too much variability to conclude that a change occurred even when means decreased; estimates over a 40-year period did show significant changes for some species and area combinations. Although the average catches for Puget Sound of chum and pink salmon are shown to be less in 1975 than the turn of the century, the inherent year-to-year variability of catch precludes a conclusive statistical demonstration of this change. Ten-year average Puget Sound catch estimates for wild chinook and coho from 1966 to 1975 (0.13 and 0.65 million, respectively) were lower than turn of the century estimates (0.34 and 1.13 million, respectively) with statistical significance exceeding $P=0.001$.

Résumé

BLEDSOE, L. J., D. A. SOMERTON, AND C. M. LYNDE. 1989. The Puget Sound runs of salmon: an examination of the changes in run size since 1896, p. 50–61. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Au cours du vingtième siècle, la mise en valeur de la région du détroit de Puget dans l'État de Washington, aux États-Unis, a influé sur de nombreux facteurs susceptibles de se répercuter sur la productivité des montaisons des saumons sauvages. La présente étude estime les indices des effectifs annuels de ces montaisons au cours d'une période dont la longueur est déterminée en fonction des données disponibles et tente de déterminer si les montaisons ont changé au fil des ans. Étant donné que les données accessibles ne remontent pas à la même époque pour toutes les espèces et régions, on a divisé la période de 1896 à 1975 en trois intervalles plus courts. Pour chacun de ceux-ci, une méthode ou plus a été employée afin d'estimer les indices de l'importance des montaisons. Des techniques de régression sont utilisées pour repérer les tendances temporelles possibles de ces indices. L'analyse n'a pas permis de déterminer avec un niveau de confiance statistique suffisant que les montaisons des saumons quinnats et cohos sauvages dans l'ensemble du détroit de Puget ont différé, de façon marquée, entre 1896 et 1975 ; toutefois, dans certaines zones du détroit, les effectifs des montaisons ont probablement diminué. Les estimations des montaisons de saumons sauvages au cours d'une période de 10 ans présentaient un niveau de variabilité trop élevé pour permettre de conclure qu'un changement s'était produit même si les moyennes avaient diminué. Les

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estimations faites pour une période de 40 ans ont révélé des changements significatifs pour certaines espèces dans certaines zones. Bien que les captures moyennes de saumons kétas et roses dans le détroit de Puget en 1975 aient été inférieures à celles enregistrées au début du siècle, il est impossible de démontrer de façon concluante par des méthodes statistiques qu'un changement s'est véritablement opéré, en raison de la variabilité inhérente des captures d'une année à l'autre. Les estimations des captures moyennes de saumons quinnats et cohos sauvages dans le détroit de Puget (valeurs établie respectivement à 0,13 et 0,65 million) au cours d'une période de 10 ans, soit de 1966 à 1975, étaient inférieures aux estimations faites pour une période équivalente au début du siècle (valeurs établies respectivement à 0,34 et 1,1 million), le seuil de signification statistique excédant $P=0{,}001$.

Puget Sound is an extensive saltwater fijord system of northwestern Washington State, United States of America, whose rivers and streams are major producers of anadromously spawning salmonid species. Since the mid 1800's many environmental factors have changed which either singly or in combination have had the potential for reducing the productivity of Puget Sound's natural runs of salmon. Stream siltation from improper logging practices, dam construction, and urbanization all may diminish the spawning habitat available to salmon. The tremendous increase in hatchery production may also be detrimental to natural salmon runs either by subverting their genetic integrity, by intensifying interspecific or intraspecific competition and predation, or, in conjunction with the increasing trend in fishing effort, by contributing to their over-harvest.

With all of these apparent environmental burdens, one expects to see a decrease in the size of wild salmon runs over time. However, such a decrease has yet to be demonstrated for Puget Sound salmon runs. Our objective then is to examine the historical record of commercial fishing on all five species of salmon occuring in Purget Sound (chinook, *Oncorhynchus tshawytscha*; coho, *O. kisutch*; chum, *O. keta*; sockeye, *O. nerka*; pink, *O. gorbuscha*), to estimate their run sizes over as long a period as data allow, and to determine whether or not they are now significantly less abundant than in former times.

There are a number of complications to achievement of even a modest subset of this objective. There could be various definitions of "run size" and various indices or proxies for a given definition. Puget Sound consists of a number of more or less discrete fishery areas including both terminal and mixed stock fisheries. The data indicative of run size exists with various degrees of precision and resolution back to the earliest official records in 1896. Both inherent variability in salmon populations, as well as apparent variability due to errors in records and failure to meet assumptions associated with operational definitions of "run size" and its proxies, will tend to mask any trend in abundance. With these problems in mind we have attempted to make such operational definitions as are necessary and expedient and come up with a "best possible" picture of the availability of salmon which extends back to the beginning of this century.

Materials and Methods

Puget Sound is defined for purposes of this study as all saltwater areas of Washington State, USA, which are east of Neah Bay (124°, 38′ W. Lon., 48°, 22′ N. Lat.). This includes the American waters of the Straits of Juan de Fuca and those surrounding and north of the San Juan islands which are normally considered as outside Puget Sound proper by most map makers and authors. It specifically excludes all of the Pacific Ocean coastal waters of Washington State.

Puget Sound salmon are subjected to a variety of fisheries as they migrate from feeding areas in the North Pacific to their natal streams. As they enter coastal areas, salmon are first caught by troll fisheries. However, these fisheries are primarily directed at chinook and coho and take only a relatively small number of pink, chum and sockeye salmon. As they traverse the Straits of Juan de Fuca and proceed on to Bellingham Bay, Skagit Bay and Puget Sound, salmon pass through gillnet and purse seine fisheries. After entering their streams, salmon are subject to capture by Indian set nets. Salmon which escape this last fishery must then successfully negotiate the streams to arrive at their spawning grounds.

Although this is a highly idealized scenario of the fisheries on Puget Sound salmon, it shows the relatively complex nature of these fisheries and it provides a framework upon which methods for estimation of salmon run size can be based. The size of a salmon run is the number of fish that would have escaped to their natal streams had there been no fisheries in that year. Except for a minor correction for mortality in coastal water, this equals the catch of a particular run by all fisheries plus the number escaping. This simple definition belies the difficulty in estimating run size, because salmon caught progressively further away from their spawning area are mixed with a greater number of fish bound for other areas. Apportioning the catch of each fishery to the appropriate run is the primary obstacle to estimation of run size.

Because of the large number of individual stocks in Puget Sound, roughly equivalent to the number of streams, we have grouped the stocks according to five terminal areas. These are geographically discrete embayments containing one or more salmon catch reporting areas designated by the Washington Department of Fisheries (WDF). A terminal area stock is defined as the group of fish which were spawned in any of the streams draining into a terminal area.

Five terminal areas are defined which cover all of Puget Sound: Hood Canal, South Puget Sound, Port Susan, Skagit Bay and Bellingham Bay. These areas along with their corresponding WDF salmon catch reporting areas, are listed in Table 1. Areas of Puget Sound not classified as terminal areas are considered to be mixed stock areas. These are seaward of terminal areas and are primarily areas through which most fish pass on the way to their respective terminal area. There are three mixed stock areas, Admiralty Inlet, Strait of Juan de Fuca and San Juan Islands, which are listed along with their associated WDF catch reporting areas in Table 1. Salmon fisheries which occur in the ocean and mixed stock areas will be referred to collectively as "intercepting fisheries", as opposed to terminal area fisheries.

For convenience, we consider a run to consist of three components: escapement to the natal stream, terminal area catch and catch by intercepting fisheries. When all three components are included in an estimate of run size, we refer to it as "ocean run size". In many situations it was impossible to apportion the catch by intercepting fisheries to the appropriate terminal areas, consequently the estimate consists only of terminal area catch and escapement. Since this estimate represents the total number of fish entering a terminal area, it is referred to as "terminal run size".

The runs of chinook and coho, and to a lesser degree, chum, contain hatchery as well as wild fish. Since it is the number of wild fish in which we are primarily interested, we use several methods to separate the wild and hatchery components of run size. In the following, whenever either component is being specifically referenced, it will be denoted with an appropriate identifier. Thus we refer to "wild terminal run size" or "hatchery

TABLE 1. Puget Sound areas utilised for summary statistics and the associated catch reporting aread numbers and names designated by the Washington Department of Fisheries. Names of salmon hatcheries in the areas are also listed. Numbers in parentheses following some names are old area codes used prior to revisions made during the 1950's.

Area	Number	Name and/or River	Hatcheries
Hood Canal (Terminal)	12	N. Hood Canal	George Adams
	12C	Central Hood Canal	Hood Canal
	12E	S. Hood Canal	
	12D	Southeast Hood Canal	
	12A	Quilcene Bay	
	12B	Dabob Bay	
	82G	Skokomish River	
South Sound (Terminal)	10	Meadow Point	Issaquah
		Rolling Bay (515)	Green River
	10C	Lake Washington	Puyallup
	10A	Elliott Bay	Minter Creek
	10E	Port Orchard	Deschutes
	10B	Shilshole Bay	Western State
	80B	Duwamish River	
	11	East Passage	
		West Passage (523)	
	11A	Commencement Bay	
	81B	Puyallup River	
	81C	White River	
	13, 13A	Carr Inlet	
	13B	Squaxin Island	
		Budd Inlet (543)	
		Case Inlet (550)	
		Eld Inlet (552)	
		Hammersley Inlet (553)	
		Totten Inlet (555)	
	83D	Nisqually River	
Port Susan (Terminal)	8C, 9A	Port Gardner	Skykomish
	8B	Port Susan	
	8A	Saratoga Passage	
	78F	Sohomish River	
	78G	Stillaguamish River	

TABLE 1. (continued)

Skagit Bay (Terminal)	8	Skagit Bay	Skagit
	78D	Skagit River	
Bellingham Bay (Terminal)	7B	Belligham Bay	Nooksack
	77	Upper Nooksack	Samish
	7C	Samish Bay	
Admiralty Inlet (Mixed)	9	Admiralty Inlet	
		Point to Point (512, 507)	
Strait of Juan de Fuca (Mixed)	5, 6C	Clallam Bay	
	6B	Discovery Bay	
		Dungeness (505)	
	6	Port Angeles	
	6A	West Beach	
	76A	Dungeness River	
	76B	Elwha River	
	76D	Salt River	
	75C	Hoko River	
	75E	Pysht River	
	75F	Sekiu River	
	75B	Deep Creek	
	74B	Sail River	
	75A	Clallam River	
San Juan Islands (Mixed)	7A	Point Roberts	
	7	Rosario	
		Salmon Banks (517)	
		San Juan Chain (518)	
		Stuart Island (521)	

ocean run size''. We assume that hatchery production of pink and sockeye salmon is negligible.

The most recent data utilized in this analysis was for 1975. The data sets which were used to estimate the various components of run size do not all extend backwards to the same point in time. To fully utilize these data the total period for which any data was available, 1896 to 1975, was divided into three periods each of which is spanned by some subset of data. These periods were selected according to the types of data available which, in turn, determined the methods of analysis and type of information which could be derived from them. All data sets were from one of seven data sets originating with the WDF; Table 2 summarizes the sources of data. The most extensive single data set, referenced in Table 2 as ''WDF catch statistics'', are unpublished records which were supplied by the Washington Department of Fisheries, mostly in the form of microfiche copies of tabular summaries. Other data sources are informally published progress reports, technical reports and annual reports of the WDF as well as personal communications with WDF personnell. The reports are available either directly from the WDF or at the Fisheries and Oceanography library of the University of Washington.

Time Periods and Methods of Summary

Period one, 1965 through 1975, was chosen because of the availability of results of tagging studies for Chinook and Coho, enabling estimation of ocean run size. Tagging studies enable apportionment of ocean and mixed area catches to appropriate terminal areas as well as separation of wild and hatchery runs from the total. Method 1, estimating ocean run size, applies to chinook and coho species for this time period. Method 2, estimating terminal run size of chinook, coho and chum, does not use tagging information or hatchery releases. It does not directly separate wild versus hatchery portions of the catch, but assumes that this ratio is the same as the ratio of wild to hatchery escapement, based on estimates of total stream and hatchery escapement.

Period two, 1935 to 1975, uses method 3 for species-time-area combinations for which wild escapement is not directly recorded but can be estimated from catch per unit effort data. This method estimates terminal area run size based on regressions of gill net catch per unit effort, where such regressions are statistically significant (estimated correlation coefficient significantly

TABLE 2. Sources of data associated with the different time periods and methods of summary referenced in the text.

No.	Data type	Year	Species	Source
1	Commercial catch	1935–75	All	WDF catch statistics
2	Wild escapement	1965–75	Chinook, Coho	WDF Tech. Rept. 28, 29
		1968–75	Chum	Jim Ames, WDF, pers. comm.
		1959–75	Pink	Jim Ames, WDF, pers. comm.
3	Hatchery escapement	1939–60	Chinook, Coho, Chum	WDF Annual Rept., 1970
		1960–75	Chinook, Coho, Chum	WDF Prog. Rept. 59
4	Contribution Rate[a]	1971–73	Chinook, Coho	WDF Prog. Rept. 49
		1964–66	Coho	WDF Prog. Repts. 1970 WDF Prog. Rept. 1971
5	Puget Sound Commercial catch	1913–34	All	WDF Annual Rept. 1936, 1937, 1938, 1939
6	Puget Sound Salmon Pack	1896–34	All	WDF Annual Rept. 1936, 1937, 1938, 1939
7	Hatchery release	1939–75	All	Tony Rasch, WDF, pers. comm.

Study periods and methods

Method	Years	Data Sources	Run size index
1	1965–75	1, 2, 3, 4, 7	Ocean wild run size
2	1965–75	1, 2, 3	Terminal wild run size
3	1951–75 1935–75	1, 3	Terminal wild run size with estimated wild escapement
4	1896–34	5, 6	Puget Sound catch

[a] Contribution rate is the fraction of the catch of a species in a mixed area and during a specific season which is estimated by tagging methods to have been from a particular stream.

different from zero) and the regression coefficient are in appropriate ranges (i.e., slope significantly different from zero and intercept not different from zero) for the catch equation (Ricker 1975). For some species-area combinations, the data needed for method 3 extends back only to various dates in the late forties or early fifties; for uniformity, estimates for these data sets are made beginning in 1951.

Period three, 1896 to 1934, includes the early period in which no direct records of fish catch were recorded. During this period, cases of salmon packed in the Puget Sound region were recorded by species. Beginning in 1912, catch was also recorded. Method 4 uses empirical regression equations to relate cases packed to catch so that a record of catch estimates could be made for period 3. This was concatenated with later catch records to form a time series for the entire period from 1896 to 1975. The regression procedure was a stepwise addition of the most significant two of the following six independent variables: the pack during a particular year, the square or cube root of the pack, the square or cube of the pack or the pack times the year.

The equations used to estimate the various run-related statistics are the standard methods associated with estimation of population sizes from tag-release data, catch-effort data (Ricker 1975; Seber 1982) and the obvious additions and subtractions implied by the definitions in the above paragraphs. The equations are not complicated but appear to be so because of the subscripts required by the many combinations of run data, areas, tag recoveries, wild versus hatchery distinctions and species. A detailed explanation of these equations, as well as further details concerning sources of data, is available as a technical report (Bledsoe et al. 1979) by request to the first author.

The size of a salmon run typically fluctuates between years due to a variety of natural causes. Annual deviations about some average run size, which may be either essentially random or strongly cyclic as exemplified by pink and sockeye salmon, account for much of this variability. Superimposed on this variability may be increasing or decreasing time trends of the average run size. In order to detect such trends, statistical methods which compare the annual fluctuations about the overall mean with a hypothesized empirical linear trend over a time period were utilized. Statistical tests then determine whether or not the estimated changes in run size over the period might have occurred by chance alone, given the year-to-year variability.

Linear regression analysis (Dixon and Massey 1983) was used to find the straight line which best fits each set of run size estimates. This method was used as an empirical, linear smoothing method, not because of any underlying hypothesis concerning a linear mechanism of population change over years. If the slope of this line is significantly different from zero, then a conclusion of change in average run size is suggested. This is in contrast to the more rigorous requirements for use of linear regression analysis for a successful application of the catch equation in method 3. The criteria of significance used uniformly for all statistical tests is that the probability of obtaining the stated condition (e.g., slope or intercept greater than zero) by chance alone is less than 0.05, referred to as the alpha level in tables. Assumptions concerning the statistical properties of the data which are necessary for validity of this test include approximate normal distribution of residuals and lack of serial correlation. In a random sub-set of 20 of the data sets used in the study, chi-square tests failed to demonstrate lack of normality though five data sets had one to three outlying data points. Pairwise serial correlation coefficients were clustered about zero; about equal numbers were negative and positive and none exceeded 0.5 in absolute value.

Three factors affect the significance level of an estimated slope; the magnitude of the actual slope, the degree of variability in run size between years and the number of years of data considered. Although a slope may appear to be quite large, the data may be so variable that the slope is not significantly different from zero by the statistical criterion. Some species show inherently less annual variability in their run sizes (e.g., chinook), consequently small changes have a relatively greater chance of being detected. A measure of the sensitivity of the test of significance, the power of the test, is the probability that a change of a given magnitude, if present, could be detected given the level of variability of the data. For each test of a time trend the power to detect a 50% change in run size from the beginning to the end of the period is reported.

To consider the possibility of a non-linear trend in run size, a quadratic coefficient of a three term multiple linear regression equation is also estimated. This is the coefficient of the independent variable (time) squared and is also tested for significance with the same criteria as the linear coefficient. Significance of this term is reported in the text for those few cases where non-linear trends occur. Each of the time trends was also graphed and examine visually, with the linear and quadratic trend estimates superimposed, in order to detect any other features or anomalies not measured by the statistical tests. These graphs are contained in the technical report (Bledsoe et al. 1979).

Results

Period 1, 1965–75

The estimates of wild ocean run size produced by method 1 and wild terminal run size produced by method 2 resulted in estimates of slope for the linearly smoothed data which are summarized in Table 3. Time series of published escapement data for coho, chinook and chum salmon were also tested for time trends in all five terminal areas. None showed significant linear or quadratic trends; 6 of 15 had positive linear coefficients and 9 were negative. The significance level of the *F* statistic test for a non-zero slope is reported; values less than 0.05 should be considered significant. The correlation coefficient, which also gives the sign of the estimated slope, and the probability of being able to detect a 50% change in run size ("power of test"), given that such a change actually occurred, are also reported.

Table 3 shows that few linear time trends are statistically detectable. The coho wild run size estimates produced by both methods 1 and 2 show no linear time trend in any area. The terminal run size (method 2) did show a significant quadratic term for Skagit and Bellingham Bay coho (alpha values of 0.03 and 0.02, respectively). This indication of a non-linear trend resulted from a generally declining trend until about 1973, followed by an increase (Fig. 1); the increase could have been a result of management actions following the Boldt decision which allowed more fish to enter these two bays. Chum terminal run size estimates do not display either a linear or quadratic time trend in any area. Chinook, however, did show a significant linear decrease in ocean run size in Port Susan. A similar, barely non-significant trend was evident in the terminal run size. Chinook show a very significant increasing trend in both ocean and terminal run sizes in Bellingham Bay. This increase, in the linearly smoothed indicator, was about a factor of two for ocean runs and nearly three for terminal runs. The data when combined for all terminal areas of Puget Sound did not show any significant changes over this time period.

The columns of Table 3 showing the probability of detection of a 50 % change in run size indicate a generally low power for these tests. This is a result of relatively high year to year variability and a relatively short time span with few data points. In only two cases did the power rise above 60 % (Port Susan chinook for methods 1 and 2); in both of these cases significant linearized trends were shown. In general, for the other areas, it is not possible to conclude that no change has occurred over the eleven year period, merely that such a change, if present, is not demonstrable by the data records and methods used in this study.

TABLE 3. Significance levels, correlations and power of test for linearly smoothed time series in wild ocean (method 1) or terminal (method 2) run size over the period 1965 to 1975. Alpha is the probability that the estimated slope would have been produced if the true slope were zero (same as significance level); power is the probability of detection of a 50 % change in the estimated run size if such a change actually occurred. The correlation coefficient, *r*, has the same sign as the estimated slope; r^2 (not given in table) is the fraction of total variation explained by the linear regression.

		Method 1 Ocean run			Method 2 Terminal run		
Species	Terminal area	alpha	*r*	power	alpha	*r*	power
	Hood Canal	.45	.25	.13	.72	−.12	.13
	South Sound	.41	−.28	.15	.57	.19	.19
Coho	Port Susan	.49	.23	.09	.94	−.03	.23
	Skagit Bay	.21	−.29	.21	.11	−.50	.35
	Bellingham Bay	.09	.53	.03	.94	−.03	.09
	Hood Canal	.92	.03	.09	.03	.49	.09
	South Sound	.41	−.28	.25	.42	.27	.11
Chinook	Port Susan	.03	−.65	.62	.06	−.58	.65
	Skagit Bay	.25	−.38	.39	.33	−.33	.39
	Bellingham Bay	.00	.82	.06	.01	−.78	.06
	Hood Canal				.38	−.36	.19
	South Sound				.62	.21	.07
Chum	Port Susan		(no values)		.97	.00	.05
	Skagit Bay				.74	.14	.06
	Bellingham Bay				.95	−.03	.11

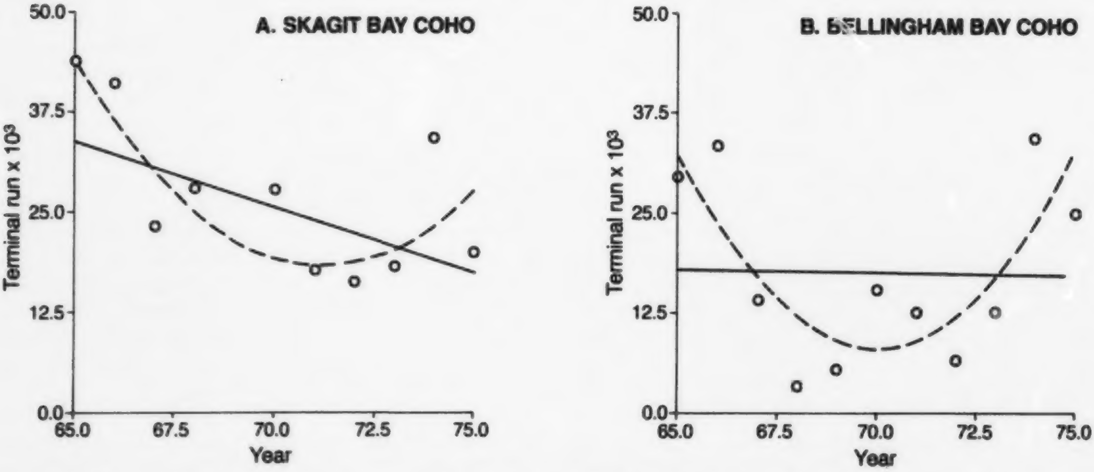

FIG. 1. Time series of terminal run size estimates from 1965 to 1975 for Skagit Bay and Bellingham Bay coho. Linear and quadratically smoothed time trends of the data are shown.

Period 2, 1935–75

Method 3 utilised regression analyses of catch on gill net effort during times of peak targetted fishing to estimate run size in each species-area combination. Hatchery catch and escapement was substracted from this estimate to produce a wild run size estimate. The estimates of wild terminal run size produced by method 3 for coho and chum resulted in estimates of linearized slope which are summarized in Table 4. Time series of estimated wild escapement data were also tested for time trends in all five terminal areas and are included in Table 4.

The use of method 3 was dependent on the statistical demonstrability of the data to estimate the coefficient of the catch equation, i.e., to demonstrate that catch is proportional to effort. For this reason, only those species-area combinations were utilized for which linear regressions of catch on effort yielded intercepts not significantly different from zero and slopes which were significantly different from zero. In addition, the criterion that the regression explain a significant fraction of the total variability was required (Dixon and Massey 1983). For coho and chum, only the Bellingham Bay data set failed the test for the regression coefficients. For chinook, though three of the five areas did not fail the test for coefficient ranges, the regression did not explain a significant fraction of the total variation and chinook was deleted from the analysis. The generally low correlation coefficients for chinook may be a result of a low rate of targetting on this species by the gill net fisheries.

The South Sound terminal run size estimates for both coho and chum show decreasing linear trends which are highly significant. By 1975 linearly smoothed values for coho wild runs in South Sound had dropped to 15 % of their 1936 level of 370 000. Chum quadratically smoothed runs had dropped to 36 % of 415 000. Quadratic smoothing, which gave an improved explanation of total variability for chum, indicated that decreases had stopped by about 1963 and that a slight, but not significant, increasing trend had begun. Skagit Bay coho also showed a decreasing trend which just missed significance (alpha = 0.056). This decrease was 33 % from a 1951 linearly smoothed level of 57 000.

The probability of detecting a 50 % decrease in run size over the period from either 1951 or 1935 to 1975 is shown in Table 4 for both species in the four terminal areas. Generally the probability levels are higher than for period 1 statistics, however they are not sufficiently high to conclude that regressions which were not significant are an indication that run size changes did not occur.

Period 3, 1896–1934

Table 5 shows the regression equations and fraction of variation explained for the relation of cases packed to recorded catch from 1913 to 1934. Data are for Puget Sound as a whole because detailed area data are not available for these early years. Catch and cases are more closely related for those species which are primarily canned (pink and sockeye) than for the species which are predominantly processed in other ways. Figure 2 showns graphically the relationship between predicted and observed catch, using the regression equations and extrapolating backwards to 1896.

Table 6 shows the time correlation and probability of a non-zero value of linear regression coefficients for the catch trend during period 3. Chinook and coho showed highly significant decreases whereas chum, pink and sockeye were not significant. The value for sockeye is nearly significant; examination of Fig. 2E clearly shows the effect of the 1913 Hells Gate slide on the

TABLE 4. Significance levels for linearly smoothed time series in wild terminal (method 3) run size and escapement values over the period 1935 or 1951 to 1975. Column headings are the same as for Table 3. There were no values for chinook because of failure of the statistical criteria for use of method 3. The method also failed for chinook and coho in Bellingham Bay. Power of test for the escapement time series was not calculated.

			Method 3 Terminal run			Escapement	
Species	Terminal area	First year	alpha	*r*	power	alpha	*r*
Coho	Hood Canal	1951	.20	−.28	.34	.01	−.51
	South Sound	1935	.00	−.73	.97	.00	−.79
	Port Susan	1935	.69	.11	.40	.13	.26
	Skagit Bay	1951	.06	−.41	.39	.21	.25
Chum	Hood Canal	1951	.78	.10	.29	.81	−.05
	South Sound	1935	.00	−.49	.59	.00	−.52
	Port Susan	1951	.67	.09	.13	.00	.47
	Skagit Bay	1951	.74	.07	.12	.05	.24

TABLE 5. Non-linear regression equations used to predict catch from packed cases of salmon during the early years of the twentieth century. N is number of salmon caught; C is the number of cases packed; Y is coded year (calendar year — 1900).

Species	Predicting equation	r^2
Coho	$N = 2.80 \times 10^{-5} C^2 - .148\ C\ Y + 8.95 \times 10^5$	.68
Chinook	$N = 7.17\ C - .205\ C\ Y + 2.37 \times 10^5$	.68
Chum	$N = 2.62 \times 10^4 C^{1/3} + 3.37 \times 10^5$	.75
Pink	$N = 19.5\ C - .255\ C\ Y$	.94
Sockeye	$N = 8.12\ C + 2.88 \times 10^{-6} C^2 + 1.55 \times 10^5$	1.00

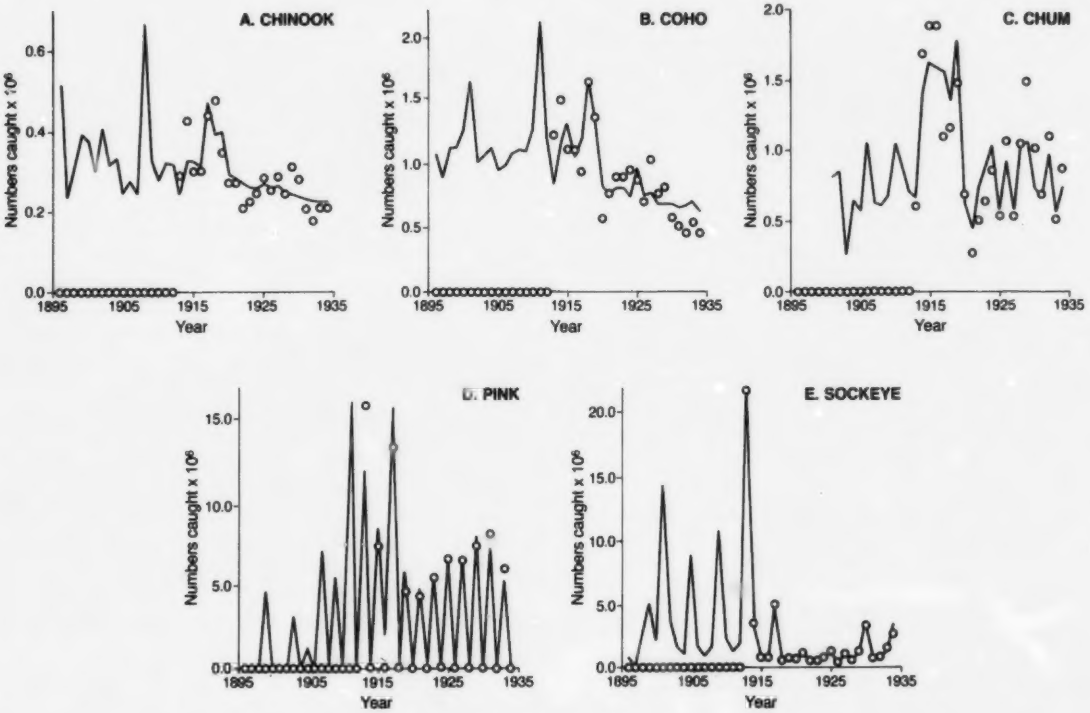

FIG. 2. Predicted and reported catch of salmonids between 1896 and 1935. Predictive equations are given in Table 5. Circles are reported catch values; solid line shows time series of yearly predicted catch.

TABLE 6. Significance levels and correlations for linearly smoothed time series of estimated Puget Sound catch over the period 1896 to 1934. Column headings are as defined for Table 3.

Species	Alpha	r
Coho	.000	−.63
Chinook	.001	−.69
Chum	.786	.10
Pink (odd years)	.485	.30
Sockeye	.088	−.22

Fraser River. Though the catch clearly diminished after the slide, a smooth linear trend is an inappropriate model to capture the effect. A non-parametric chi-square as well as a t-test showed a highly significant decrease in sockeye catch after 1915.

The catch from 1896 to 1934 can be interpreted as a good index of the actual number of fish bound for Puget Sound streams only if the following assumptions are true:

1. The 1896–1912 estimated catch is close to the actual catch. In general, the predicted catch is quite

similar to the observed catch; the extrapolated estimates of catch seem to be without significant bias.

2. Catch of Canadian fish in the Strait of Juan de Fuca and the San Juan Islands is not a significant proportion of the total Puget Sound catch. This is definitely not true for sockeye as the decrease following 1915 is due to elimination of Fraser River fish. The catches of chum and pink also undoubtedly contain a large number of fish from Canadian streams; the catches of coho and chinook probably do not.

3. Catch of fish prior to their entering Puget Sound is either small or approximately a constant fraction of the run. From 1913 to 1934 the ocean catch of all species was relatively small, less then 10 % for sockeye, chum and pink and less than 25 % for coho and chinook.

4. Puget Sound fisheries either remove a constant fraction of the run or a varying proportion but with escapement constant. This is the single most important assumption necessary for use of time trends in catch as indicators of trends in run size. Varying economic conditions and management regulations may have resulted in serious departures from this assumption. Without additional data the magnitude of these departures cannot be assessed.

Catch is always an underestimate of run size because it does not include escapement, however catch can be regarded as a lower bound to run size with reasonable certainty, even if all the assumptions except the second are not true.

Figure 3 shows the combination of estimated and recorded catch of non-hatchery salmon in Puget Sound from 1896 to 1975.

Discussion

From the foregoing it is clear that, at least over the period from 1935 to 1975, a dramatic general decrease in the wild runs of Puget Sound coho, chinook and chum salmon cannot be demonstrated statistically. Chinook had a significant decrease of wild ocean run size in Port Susan from 1965 to 1975. Coho and chum had significant decreases of wild terminal area run size in south Puget Sound from 1935 to 1975, however an increasing trend of prior interceptions is very likely during this period.

The most substantial evidence of a decrease of wild runs is the highly significant decline in total Puget Sound catch of chinook and coho salmon from 1896 to 1934. It is unlikely that this trend could be induced by prior interceptions because the coastal troll catch during this period was relatively small. If the catch to escapement ratio remained fairly constant, then a real decrease in the wild runs of chinook and coho probably occurred.

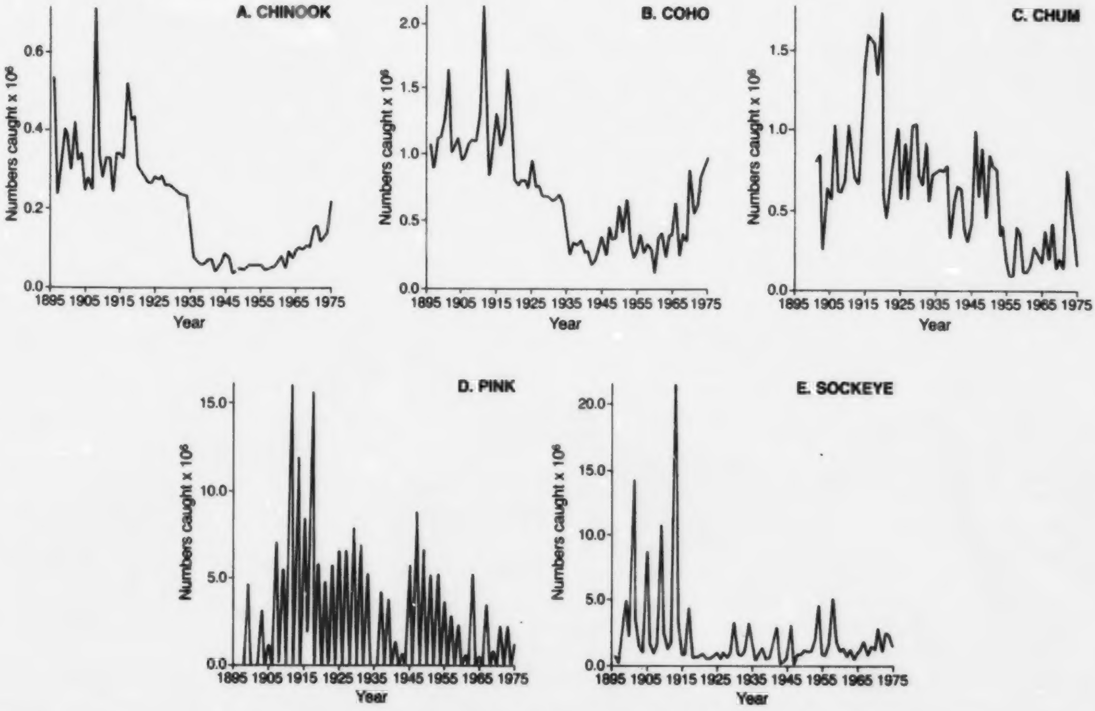

FIG. 3. Time series of estimated and reported total catch of five species of Puget Sound salmon from 1896 to 1975.

The plots of the total Puget Sound catch of chinook and coho (Fig. 3) show a conspicuous feature which does not represent changes in the abundance of wild fish. The abrupt decrease in catch starting in 1935 was the result of Initiative 77, passed by the voters of Washington State, which closed Puget Sound to the use of purse seines on chinook and coho and prohibited the use of fish traps.

A less obvious but equally significant factor affecting the Puget Sound catch of chinook and coho is the prior interception of these fish by troll fisheries off the coasts of Washington and Vancouver Island. These fisheries increased since 1935 and were partially responsible for the Puget Sound catches not returning to their pre-Initiative 77 levels. Although the data is insufficient to estimate the total troll catch (American and Canadian) before the early 1960's, based on tag returns utilised in method 1, by 1965 the Canadian troll fishery accounted for 47 % of the total catch of Puget Sound coho. By 1974, the Canadian troll fishery caught 73 % and 64 % of the total catch of Puget Sound coho and fall chinook, respectively.

Because the intercepting fisheries have probably reduced the proportion of each wild chinook and coho run returning to Puget Sound, the ocean wild runs of these species may be as large today as they were at the turn of the century. If we assume that the intercepting fisheries were negligible in 1900, and that the catch to escapement ratio which existed then to be nearly the same as it is now, then the early Puget Sound catches (estimated by method 4) can be compared to the total catch of wild Puget Sound fish in recent years (estimated by method 1). The ten year average (1896 to 1905) catch in numbers is 1.13 million for coho and .344 million for chinook. The 10-year average (1966 to 1975) catch in numbers is .648 million for wild coho and .132 million for wild chinook. This represents a decrease of 43 % and 61 %, respectively, and is statistically significant at a probability less than 0.001 (F = 22.1 and 54.9, respectively, with 2 and 18 degrees of freedom).

Though it was not possible to demonstrate changes in the wild runs to Puget Sound overall, there are specific terminal areas where this has undoubtedly occurred. For example, the chinook run to Port Susan and the coho run to South Sound have decreased.

The historical trend in the Puget Sound catch of chum salmon is similar to chinook and coho in that the catch at present is less than it was during the 1930's (Fig. 3). Chum differ from these species by being less susceptible to troll fisheries, thus this decline in catch cannot be attributed to increasing intercepting fisheries. In this case declining catches probably indicate reduced run size. In some terminal areas the downward trend in catch was more apparent than in others. From 1935 to 1975, Hood Canal and the South Sound showed no downward trend from graphic examination, whereas Port Susan, Skagit Bay and Bellingham Bay showed noticeable downward trends which were not demonstrable statistically. Mixed area catches of chum generally reflected the variability shown for chum in Fig. 3 for the entire Sound. The generally constant time series of catch for chum in the South Sound is in contrast to the highly significant downward trend in both wild run size as well as escapement levels.

The Puget Sound catch of pink salmon has declined since 1930 in a manner similar to the catch of chum salmon. Most of the Puged Sound catch of pink salmon is taken in the mixed stock areas, primarily near the San Juan Islands. Although most of these fish are bound for Canadian waters, the magnitude of this catch is so large in comparison to the rest of Puget Sound that these fisheries must take a sizeable proportion of the terminal area runs. Consequently, trends in estimates of terminal run size cannot be interpreted as trends in ocean run size without considering changes in these intercepting fisheries.

The Puget Sound catch of sockeye salmon is taken almost exclusively in the mixed stock area near the San Juan Islands (except for a small fishery for Lake Washington sockeye in the South Sound). Nearly all of these fish are bound for Canadian waters. Excluding the loss of Fraser River fish after 1913, there is little evidence of a decrease in sockeye catch or runs to Puget Sound; Fig. 3 shows a very slight tendency toward an increase in the final two decades of data.

In summary, the major value of this analysis may be in terms of the demonstration of the amount of data, in terms of years of collection, which are required to document a change in salmon runs in the face of the inherently high variability of these numbers. Ten years will rarely be sufficient; 40 years is a more reasonable objective in order to document a 50 % change in run size. A further value of this exercise is a demonstration of the importance of collection of various kinds of statistics associated with salmon fisheries. These include not only an extensive tagging program for wild and hatchery fish, but also escapement counts and accurate records of catch and effort by area. Only with such complete and long term records will it be possible in future years to analyse the fate of salmon fisheries and enable appropriate action to restore damaged stocks.

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Observed and Simulated Effects of Climatic Variability, Clear-Cut Logging and Fishing on the Numbers of Chum Salmon *(Oncorhynchus keta)* and Coho Salmon *(O. kisutch)* Returning to Carnation Creek, British Columbia[1]

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Abstract

HOLTBY, L. B., AND J. C. SCRIVENER. 1989. Observed and simulated effects of climatic variability, clear-cut logging, and fishing on the numbers of chum salmon *(Oncorhynchus keta)* and coho salmon *(O. kisutch)* returning to Carnation Creek, British Columbia, p. 62–81. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

The population dynamics of coho and chum salmon have been studied at Carnation Creek since 1970 as part of a multi-disciplinary study of the effects of logging on a small salmon stream in a coastal rainforest. We have developed models that predict the numbers of chum and coho salmon from correlative relationships between survival and growth at various life stages and (1) climatic, hydrologic and physical variables, (2) indices of those features of the stream habitat that were affected by logging and, (3) exploitation rates in the fishery. The models were used to partition the variability in adult returns between the effects of climatic variability in the stream and the ocean, changes in stream conditions caused by logging and variations in fishing mortality. For both species, most of the observed variation in adult numbers resulted from climatic variability in the stream and the ocean, and in roughly equal measure. Variation of the fishing mortality over realistic ranges did not change variability in adult abundance, except at high exploitation rates where variability was increased. Coho salmon were unaffected by observed and simulated logging activity but chum salmon were adversely affected. We suggest that overall variability in the salmon abundance will tend to increase in the wake of land-use activities, particularly when accompanied by high levels of exploitation and adverse environmental conditions.

Résumé

HOLTBY, L. B., AND J. C. SCRIVENER. 1989. Observed and simulated effects of climatic variability, clear-cut logging, and fishing on the numbers of chum salmon *(Oncorhynchus keta)* and coho salmon *(O. kisutch)* returning to Carnation Creek, British Columbia, p. 62–81. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Depuis 1970, la dynamique des populations de saumons cohos et kétas dans le ruisseau Carnation fait l'objet de recherches, dans le cadre d'une étude multidisciplinaire portant sur les effets de l'exploitation forestière sur les petits cours d'eau abritant des saumons dans une rivière ombrophile côtière. Nous avons élaboré des modèles qui prévoient les effectifs de kétas et de cohos d'après la corrélation établie, d'une part, entre la survie et la croissance à divers stades de vie et, d'autre part, 1) des variables climatiques, hydrologiques et physiques, 2) des indices des caractéristiques des habitats des cours d'eau qui ont été perturbées par l'exploitation forestière et 3) les taux d'exploitation dans les zones de pêche. Les modèles ont servi à répartir la variabilité des retours d'adultes en fonction des effets des changements climatiques sur les cours d'eau et l'océan, des changements des conditions des cours d'eau dus à l'exploitation forestière et des variations de la mortalité par pêche. Pour les deux espèces, et de façon à peu près égale, les variations observées du nombre d'adultes étaient dues, en majeure partie, aux effets des changements climatiques sur les cours d'eau et l'océan. Les variations de la mortalité due à la pêche dans des plages de valeurs réalistes n'ont pas influé sur la variabilité de l'abondance des adultes, sauf lorsque les taux d'exploitation étaient élevés, entraînant une variabilité accrue. Les saumons cohos n'ont pas été perturbés par l'exploitation forestière observée et simulée, contrairement aux saumons kétas sur lesquels cette

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[1] Contribution No. 124 of the Carnation Creek Experimental Watershed Project.

activité a eu des effets nuisibles. Nous avançons l'hypothèse selon laquelle l'utilisation des terres tendra à accroître la variabilité de l'abondance des saumons, particulièrement quand leur exploitation est forte et que les conditions écologiques sont défavorables.

Introduction

Considerable between-year variability in abundance is commonly observed in commercial fishery stocks including those of Pacific salmon (*Oncorhynchus* sp.), but for the most part the sources of this variability are uncertain. Understanding inter-annual variability in recruitment has been recognized as the most important problem in fisheries science (Sissenwine 1984a). Variability in freshwater nursery and rearing environments is thought to be an important source of recruitment variability for all anadromous species (Crecco et al. 1986; Leggett and Carscadden 1978; McNeil 1974), but particularly for those which rear for a year or more in freshwaters. Studies demonstrating the adverse effects of low stream discharge during the summer on juvenile survival and smolt production are often cited in this context (e. g. Matthews and Olson 1980; Scarnecchia 1981). Other studies have demonstrated the importance of variation in marine rearing conditions as measured through changes in such factors as upwelling, salinity and temperature (Nickelson 1986).

In addition to the effects of "natural" (i.e. climatic) variation most Pacific salmon stocks in British Columbia are exploited by commercial and sport fisheries and originate in areas where there are intensive land-based resource industries (e.g. logging, mining, hydroelectric generation, irrigation). Variations in numbers of adult salmon, and particularly perceived declines in numbers, are commonly attributed to either habitat destruction or to overfishing.

The population dynamics of coho and chum salmon have been studied at Carnation Creek since 1970 as part of a multi-disciplinary study of the effects of logging on a small salmon stream in a coastal rainforest. In this paper we describe models that predict, for both salmon species, the numbers of adult fish returning to Carnation Creek. Using those models and both observed, and hypothetical, time series of climatic variables, physical variables affected by logging and fishing mortalities, we explore the roles of climate, logging and fishing in determining adult recruitment for the two species of Pacific salmon.

Study Site

Carnation Creek (Lat. 48°55′ N; Long. 125°00′ W) is situated on the south side of Barkley Sound on the west coast of Vancouver Island. The stream is approximately 7.8 km in length but only the lower 3.1 km is accessible to anadromous fishes. The maritime climate is characterized by cool temperatures. Most of the annual precipitation (250–350 cm) falls as rain during the winter. Stream discharge varies widely over the year from summer lows of 0.02 $m^3 \cdot s^{-1}$ to winter peaks of as much as 65 $m^3 \cdot s^{-1}$.

Approximately 41 % of the watershed was clear-cut in stages between autumn 1975 and spring 1981 (Dryburgh 1982). Clear-cut logging extended to the stream edge over 60 % of the lower stream accessible to anadromous fish. Some of the different harvest treatments that were applied to the streambank in the anadromous sections damaged the streambank and destabilized both the streambank and the stream channel (Hartman and Holtby 1982; Hartman et al. 1987). The streamside logging has also caused marked changes in the thermal regime of the creek (Holtby 1988a) which in turn have had significant impacts on the coho salmon (Holtby 1988c). The objectives, design, and forestry plan of the Carnation Creek Watershed Study are discussed elsewhere in more detail (Dryburgh 1982; Scrivener 1988a).

Several physical measurements that are relevant to our study were routinely collected at Carnation Creek. Stream stage height was measured continuously by a Stevens A-71 recorder at a broad-crested hydrological weir located 400 m upstream of the fish-counting fence. The weir was operated by the Inland Waters Directorate of Environment Canada. Stage heights were converted to instantaneous discharges using a periodically calibrated rating curve. Stream temperatures were measured continuously at the same time with a Lambrecht 256C recorder. Air temperatures were measured continuously with a Lambrecht 252C recorder on a cleared hilltop located 800 m from the hydrological weir. The particle size distribution of the spawning gravel was determined every year from ~200 cores taken from nine sites distributed throughout the stream. Frozen cores to a depth of 30 cm were obtained with a modified Ryan sampler (Ryan 1970), acetone and dry ice. The cores were partitioned into surface to 14-cm and 14- to 30-cm strata, and dry sieved (Scrivener and Brownlee 1989). Geometric mean particle size (D_g) and a Fredle index were computed following the procedures of Lotspeich and Everest (1981) as described by Scrivener (1988b). Average values of D_g used in the chum model were computed for the three sampling sites in the estuary and lower stream where most of the chum spawned. The average values of the Fredle index used in the coho model were computed for five sites from 200 to 2250 m above the estuary.

Although considerable data has been collected on channel configuration and debris loading (e.g. Toews and Moore 1982), that data were not available to us in a form that could be readily related to fish abundance or mortality. We devised instead a subjective index of habitat quality (HQI) as follows. The length of the stream accessible to anadromous fishes was divided into five reaches. Four of the reaches had received different logging treatments along their streambank while the fifth was unlogged. Three field biologists with extensive experience at Carnation Creek (two have been continuously active there for the entire study), were then asked to rate habitat quality in each reach for the summer and winter of each year of the study and provide commentary on the parameters used in their judgments. The ratings ranged between 0 (no carrying capacity) to 10 (best conceivable habitat). Conditions during pre-logging were arbitrarily assigned index values of 5. The three ratings were averaged within stream reach and year. To provide a single HQI value for the entire stream, the average ratings by section were first doubly weighted, first by the lengths of the five stream reaches and then by the average, end-of-summer coho abundance ($n \cdot m^{-1}$) from 1972 to 1974. Habitat changes within long reaches heavily utilized by fish were thus more important than changes in short, less heavily used reaches. The weighted ratings were summed and standardized on a scale of 0–1 (Table 1). Two factors consistently figured in judgments of habitat quality: the number and depth of "large" pools ($> \sim 100$ m^2), and the amount of stable, large organic debris in the thalweg accessible at all stream flows. The values of HQI should not be interpreted as relative indicators of productive capacity: a value of 0.37 in 1986 (Table 1) does not mean that the productive capacity of the stream was 37 % of what it was in 1977, when HQI had a value of 1.0.

We have employed several measures of near-shore, surface temperatures and salinities for the Pacific Ocean that are routinely collected from coastal lighthouses (Dodimead 1984). Mean monthly temperatures (SST) and salinities (SSS) for Amphitrite Point lighthouse were calculated from daily measurements. A monthly salinity anomaly (SSSA) was calculated by subtracting the 50-yr mean (1934–84) for a month from the SSS for that month and year. Mean temperatures and salinity anomalies from March–June at Amphitrite Point were used as indicators of ocean conditions during the period that chum fry and coho smolts entered the ocean. Mean temperatures and salinities for October–February at Amphitrite Point were used as indicators of ocean conditions during the first winter spent in the ocean by coho juveniles.

Fish Population Studies

Two species of anadromous Pacific salmon are common in Carnation Creek. Returning coho salmon *(Oncorhynchus kisutch)* were enumerated at a fence near the stream mouth during the fall each year (Ander-

TABLE 1. Habitat quality scores by stream reach, season (S: summer and W: winter) and year and computed values of the Habitat Quality Index for the summer (HQI_S) and winter (HQI_W) for the whole stream.

	Stream Reach											
Year	I		II		III		IV		V		HQI_S	HQI_W
	S	W	S	W	S	W	S	W	S	W		
1971	5	5	5	5	5	5	5	5	5	5	0.89	1.00
1972	5	5	5	5	5	5	5	5	5	5	0.89	1.00
1973	5	5	5	5	5	5	5	5	5	5	0.89	1.00
1974	5	5	5	5	5	5	5	5	5	5	0.89	1.00
1975	5	5	5	5	5	5	5	5	5	5	0.89	1.00
1976	5	5	5	5	5	5	5	5	5	5	0.89	1.00
1977	5	5	5	5	7	5	5	5	5	5	1.00	1.00
1978	5	5	5	5	7	5	3	2	5	5	0.93	0.88
1980	5	5	5	5	5	4	3	2	4	4	0.77	0.76
1981	5	5	5	4	5	4	3	2	4	4	0.74	0.75
1982	4	4	5	4	5	4	3	2	3	4	0.69	0.75
1983	4	4	5	4	3	3	2	1	2	2	0.47	0.49
1984	3	4	5	3	3	3	2	1	0	1	0.37	0.44
1985	3	3	5	3	3	3	2	0	0	1	0.37	0.37
1986	3	3	5	3	3	3	2	0	0	1	0.37	0.37
section length (m)	567		349		493		798		767			
end of summer coho abundance (both age-groups summed) ($n \cdot m^{-1}$)	3.22		2.20		7.64		2.91		4.4			
section weighting	0.151		0.063		0.308		0.202		0.274			

sen 1983, 1984, 1985). Adults were individually measured, sexed and a scale age including freshwater age was determined. The number of spawners has varied from 74 (1984) to 426 (1979) with a typical escapement of 230 fish. Spawning occurred in all areas of the stream accessible to anadromous fishes. A size-fecundity relationship for the 1975 brood from the nearby Robertson Creek hatchery, augmented by measurements from four Carnation Creek females, was used to estimate total egg deposition (Holtby and Healey 1986). The fry and smolts migrating downstream were enumerated from early-March through August each year. At intervals of 7–10 d, the fork-lengths (FL) of at least 50 fry were measured to the nearest mm, and ~20 smolts spanning the observed size range were weighed to the nearest 0.1 g and aged using scales. The FL of all smolts were measured to the nearest mm. The size-age relationship developed was applied to all of the smolts of that year. Three times each year, in mid-May, late-July and mid-September, the total number of fry and fingerlings resident in the stream was censused in six sections, each 32–113 m long (average 55 m), by intensive pole seining and electroshocking (Andersen 1983). On average 11 % of the accessible stream was censused. Section boundaries were always natural habitat features and were adjusted each year as channel configuration and the location of large debris varied. The lower 3.1 km of the stream was geomorphically uniform prior to logging, and the study sections were chosen so that reaches affected by, or isolated from, the different logging protocols were included. Catches for all sections were pooled and the number of fish in the sections was estimated by the removal method (Seber and LeCren 1967). The total stream population was obtained by multiplying the estimate for sections censused by the ratio of uncensused to censused stream length. During each census, fingerling fork-lengths were determined to the nearest mm, a representative sub-sample of fish were weighed to the nearest 0.1 g and a size-age relationship was determined from scale samples. Total annual emergence of coho fry was obtained by summing the number of fry in the May census with the number that had emigrated through the counting fence prior to the census.

We have no direct measure of the number of coho caught in the sport and commercial fisheries and hence, no measure of the magnitude of natural mortality. However, it has been possible to estimate mortality due to the fishery using data gathered from coded-wire tagged releases of coho from the nearby Robertson Creek Hatchery from 1974-present (Holtby 1988c). The use of time series of natural and fishing mortalities from Robertson Creek hatchery necessitates the important but untestable assumption that the hatchery smolts behaved similarly to smolts from Carnation Creek. The assumption that hatchery stocks can be used as indicators of wild stocks has been widely made but is only now being critically examined through field experimentation (C. Walters, Univ. British Columbia, Vancouver, B.C., pers. comm.).

Most of the returning chum salmon *(O. keta)* spawn in a 300 m stretch that extends from minimum high tide to the upper edge of salt water intrusion at the counting fence. In most years some chum salmon (3–30 %) spawned above the counting fence. Numbers in the estuary were estimated from visual counts made by experienced observers 3–5 times during the 2-wk period of spawning. The same observers have been present throughout the study. The chum salmon usually spawned within 2 d of entering the stream and new immigrants were easily distinguished from previously counted adults by their bright colors and fresh appearance. There have been frequent replicate counts and between observer comparisons all of which indicate that the estimated numbers are precise. Escapement has ranged from 290 (1986) to 4168 (1973). In most years escapement was between 1200 and 2100. The age composition of spawning chum salmon was determined every year by examining approximately 200 otoliths (Bagenal and Tesch 1978) collected during carcass sampling immediately after spawning. Most fish are age 4 (~80 %) with some age 3 (~15 %) and age 5 (~5 %), and the age structure was stable for the duration of our study (Andersen 1983). Size distributions and sex composition were also determined during the carcass recovery. A size-fecundity relationship for chum spawners was determined from 30 females that were sacrificed in 1980, 1981 and 1983. Total egg depositions above and below the fence were calculated using that relationship and the size-frequency distributions of the females. The numbers of chum salmon fry emerging above the fence and their emigration timing were obtained from the counting fence each spring. Fry lengths were estimated from samples of at least 50 fish taken every 7–10 days. Each year 20–30 emergence traps were placed below the fence. Fry caught in the traps were counted and measured daily. The emergence timing and size of fry caught in the emergence traps are very similar to the timing and size of fry intercepted at the fence (Scrivener 1988b).

Fisheries on Barkley Sound chum salmon stocks are thought to have had little impact on the Carnation Creek population. There is a native food fishery off the mouths of Sarita River (1.8 km S of Carnation Creek) and Carnation Creek which takes up to ~300 fish, some of which are probably Carnation Creek fish. The native fishery is very small, often consisting of one drift net set during the peak of the run, and it has been concentrated on the Sarita River. Commercial harvesting in Barkley Sound has been restricted since 1962. The exploitation rate has been less than 1 % in 15 of the last 24 years and less than 15 % in 20 of those years (Lightly et al. 1985). In the four remaining years, (1971, 1973, 1978, and 1980), exploitation ranged from 20 to 43 %.

The extensive fishery in those years reflected exceptional returns to Barkley Sound (Lightly et al. 1985) and also years of high escapements to Carnation Creek (Andersen 1983). The commercial gillnet and seine fisheries are concentrated in terminal areas on the north side of Barkley Sound (Lightly et al. 1985). The location of the commercial harvest suggest that few Carnation Creek fish were caught.

Model Parameterization

Models that predict adult escapements were developed for both species of salmon. The models utilize a sequentially linked series of regression models that predict survival and fish size at different life history stages from various physical variables. The numbers and size of spawners serve as inputs to the models.

Chum Salmon Model

The model predicting the number of returning adults (Fig. 1) is comprised of seven sub-models, each of which is discussed below.

Sub-model 1 predicts total egg deposition from the number of females, the female fork-length frequency distribution and the following fecundity–FL relationship:

$$(1)\ \log_{10}\text{Fecundity} = 2.0506 \cdot \log_{10}\text{FL (cm)} - .3873 \quad (r=0.741,\ n=30,\ P<0.001).$$

The fecundity–FL relationship is similar to others for this species (Koski 1975; Beacham 1982). The proportion of spawners that were female ranged from 0.29 to 0.51 (mean: 0.429).

Sub-model 2 predicts egg-to-fry survival from geometric mean particle sizes of the gravel (D_g) in the estuary and lower creek:

$$(2)\ \%\text{Survival}_{\text{gravel}} = 3.436 \cdot D_g - 34.431 \quad (r=0.674,\ n=14,\ P<0.01).$$

Egg survival is known to be adversely affected by the reduction in permeability and interstitial spaces that results from the presence of fine particles (< 10 mm dia.; Everest et al. 1987). Excessive quantities of fine particles reduce the movement of alevins within the gravel and can create barriers to emergence (Koski 1975; Scrivener and Brownlee 1982; Wickett 1958). It is thought that the relationship between gravel particle size and chum salmon egg-to-fry survival observed in Carnation Creek is due largely to entrapment rather than oxygen deprivation (Scrivener and Brownlee 1982, 1989). Egg-to-fry survivals were observed only for those eggs deposited above the counting fence, a

CHUM MODEL

sub-model	output=fn(inputs)	function output is affected by:			
		density	climate		logging
		dependence	freshwater	marine	
1	fecundity = fn(female fork-length) #eggs deposited = fn(#females, fecundity)				
2	egg survival = fn(gravel particle size)		○		●
3	#emergent fry = fn(#eggs deposited, egg survival, #spawners)	●			
4	#recruits = fn(#emergent fry, emergence date, sea surface salinity, fry size)	●		●	
5	fry size = fn(female size, peak discharge)		●		○
6	emergence date = fn(spring thermal summation)		●		●
7	female size = fn(fry size, sea surface temperature)	○		●	

FIG. 1. Major components of the chum salmon population model. The important modifiers of each relationship are shown by a closed circle, where we detected the effect in this study, an open circle, where the effect has been detected elsewhere and may have been present in Carnation Creek, or no symbol, where no effect was expected or detected.

fraction of the total egg deposition that ranged from 0.01 to 0.13 with a mean of 0.048. Chum spawners above the fence were distributed throughout the lower km of the stream and consequently spawner densities above the fence were always below the threshold value (~ 1 female$\cdot 15$ m^{-2}), required to reduce egg survival through spawner density effects (Hunter 1959). Predation on emergent fry likely occurred between the time of emergence and the time that they were counted at the fence. The magnitude of that predation is unknown but we have assumed that it varied randomly over the course of the study.

Sub-model 3 corrects for the effects of spawner density on egg-to-fry survival. We used the data presented by Hunter (1959) to estimate egg-to-fry survivals as a function of egg density:

$$(3)\ \log_{10}\%\text{Survival} = -0.0002203 \cdot \text{Egg density } (\text{m}^{-2}) + 1.4282$$
$$(r=0.840,\ n=11,\ P<0.002).$$

For spawners below the fence, egg densities were calculated by dividing the total egg deposition predicted by sub-model 1 for the spawners below the fence, by 1800 m^2, the approximate spawning area below the fence. Inter-annual variability in the area available for spawning was probably small. The immediate stream-side was not logged and changes in channel configuration were confined to minor alterations in depth (Toews and Moore 1982; L. Powell, Fisheries and Oceans, Vancouver, unpubl. data). Estimated survivals from the above equation were then standardized by dividing by 24.2, the mean % survival observed by Hunter (1959) at spawner densities below the threshold for density-dependent effects. Total fry production was then estimated as the sum of the production above the fence:

$$(4)\ \text{Fry}_{\text{above}} = 0.01 \cdot \text{Egg deposition}_{\text{above}} \cdot \%\text{survival}_{\text{gravel}}$$

and production below the fence:

$$(5)\ \text{Fry}_{\text{below}} = \text{Egg deposition}_{\text{below}} \cdot \%\text{survival}_{\text{gravel}} \cdot \text{standardized sub-model 3 survival.}$$

The application of sub-models 1–3 to the observed time series of female escapements produced a time series of total fry production.

Sub-model 4 predicts total brood-year return from estimated fry production and three independent variables: the date of median fry emigration (JD_{50}), the mean fry FL (FL_{fry}), and the surface salinity anomaly at Amphitrite Point during the period of fry migration ($SSSA_{spr}$):

$$\begin{aligned}(6)\ \log_{10} N_{\text{recruit}} = -8.569 &+ 0.4659 \cdot \log_{10} N_{\text{fry}} \\ &+ 0.215 \cdot SSSA_{\text{spr}}\ (‰) \\ &+ 1057 \cdot FL_{\text{fry}}\ (\text{mm}) \\ &+ 23.36 \cdot JD_{50}\ (\text{Julian}),\end{aligned}$$
$$(r=0.93,\ n=13,\ P<0.001).$$

The independent variables were selected *a priori* as likely correlates of fry survival with the following reasoning. The important predators on chum fry are probably piscivorous fishes with much of the predation occurring in the first 40 days of ocean life in estuaries and near the shore (Hunter 1959; Parker 1971) or during the transition from near-shore to the pelagium (Healey 1982). Predation rates are negatively size-dependent (Hargreaves and LeBrasseur 1985, 1986; Healey 1982). We infer that the larger a fry is when it enters the ocean the more likely it is to survive and that mean fry FL should be a correlate of mean survival. It should also be true that predation losses are negatively correlated with growth rates and therefore, factors which affect growth rates should be correlated with survival. Walters et al. (1978) argue that fry entering the ocean must do so within a time-window that coincides with the vernal peak in estuarine and near-shore productivity. The fry do so in order to maximize food availability and thereby maximize their growth rates and minimize the time that they are of the size most vulnerable to predators. It is also possible that fry migration is synchronous within a general geographical area in order to maximize predator saturation and minimize losses to predation. Both hypotheses are consistent with the observation that fry emergence and emigration are synchronous for early and late spawning stocks within broad geographic areas (Hunter 1959; Koski 1975; Beacham and Murray 1986). Regardless of which hypothesis is more generally applicable, we infer that fry emigration timing should be a correlate of survival. Finally, it is known that changes in oceanic circulation patterns off the west coast of Vancouver Island affect the distribution of predators and of zones of upwelling and high plankton productivity (Fulton and LeBrasseur 1985). In years characterized by high surface temperatures and low surface salinities (negative anomalies) the subarctic boundary, the interface of the Alaskan gyre and the California Current system and a region of high zooplankton abundance, shifts northward and away from the coast of Vancouver Island. Fulton and LeBrasseur (1985) speculate that this could cause reduced growth and increased mortality of juvenile salmonids off the coast of Vancouver Island. This being so, chum fry survival should be correlated with the salinity anomaly in the surface layers.

All four of the parameters in sub-model 4 were significant and direction of the indicated effects was as expected. The parameter estimate for the fry FL term suggests that the effect of size on survival is very large indeed: within the observed range of FL (41.6–43.3 mm), and increment of one mm in length was associated with an increase in recruitment of 596 fish. The apparent effects of the factors associated with the salinity anomaly were also large. Over the range of the anomaly observed (−1.2 to 0.3), a decrease of 1‰ was associated with a reduction in recruitment of 1452 fish. Changes in emigration timing were also associated with large changes in recruitment. Varying the median date of fry emigration over the observed range of 50 days was associated with a change in recruitment of 1050 fish.

Sub-model 5 predicts fry FL from female FL and from peak stream discharges during egg incubation:

$$(7)\quad FL_{fry}\ (\text{mm}) = 20.55 + 0.278 \cdot FL_{female}\ (\text{cm}) + 0.300 \cdot \text{Peak discharge}\ (\text{m}^3 \cdot \text{s}^{-1})\quad (r=0.77,\ n=16,\ P<0.02).$$

The level of explained variance is low however, especially considering the importance of very small increments in fry size that are indicated in sub-model 4. Fry size varies with female FL in accordance with the general dependence of egg size on female size. Fry size is thought to depend on gravel quality (Koski 1975; Scrivener and Brownlee 1989) but there was no direct statistical evidence of such an effect in this study. However, during large peak discharge events, fine particles were flushed from the surface layers of the gravel (Scrivener and Brownlee 1989). Improvement in gravel quality after large freshets might have increased the emergence success of large chum fry.

Sub-model 6 predicts the median day (Julian) of fry emigration (JD_{50}) from February-March thermal summations (CTS_{spr}) at the main hydrological weir in Carnation Creek:

$$(8)\quad JD_{50} = -0.2043 \cdot CTS_{spr} + 162.29,\quad (r=0.876,\ n=14,\ P<0.001).$$

Sub-model 7 predicts the mean FL of returning adults from mean fry FL and from sea surface temperatures at Amphitrite Point around the time of migration (SST_{spr}):

$$(9)\quad FL_{adult}\ (\text{cm}) = 161.64 - 1.927 \cdot FL_{fry}\ (\text{mm}) - 1.027 \cdot SST_{spr}\quad (r=0.838,\ n=13,\ P<0.005).$$

There is no obvious explanation of the tendency for large adults to return from small fry. Years of high sea surface temperatures also tended to be years of large negative salinity anormalies. Not only did fewer fish return during those years (sub-model 4) but they were smaller as well.

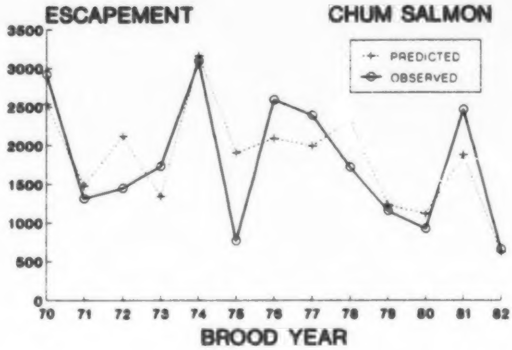

FIG. 2. Observed and predicted escapements of chum salmon adults to Carnation Creek. All age-groups were combined.

The model performs reasonably well in predicting total recruitment when given the observed time series of spawner number and size and time series of all of the independent physical variables (Fig. 2; $r=0.782$ correlation of predicted and observed recruitment, $n=13$, $P=0.0016$).

Coho Salmon Model

The model developed to predict the numbers of returning coho salmon is comprised of 12 sub-models (Fig. 3). The model is similar to the one presented by Holtby (1988c), but has been expanded to include all life stages.

Sub-model 1 predicts the numbers of emergent fry from the numbers and sizes of females and peak winter discharges during egg incubation:

$$(10)\quad \text{a. } \log_{10} \text{Fecundity} = 2.914 \cdot \log_{10} FL_{female}\ (\text{cm}) - 1.951$$

$$(11)\quad \text{b. Total egg deposition} = N_{females} \cdot \text{Fecundity}$$

$$(12)\quad \text{c. } \%\text{Survival}_{egg} = 1 - 1.091 \cdot \text{Peak discharge}\ (\text{m}^3 \cdot \text{s}^{-1}) / (12.75 + \text{Peak discharge}),\quad (r=0.651,\ n=16,\ P<0.01).$$

$$(13)\quad \text{d. } N_{emerge} = \%\text{Survival}_{egg} \cdot N_{egg}.$$

The relationship between egg mortality and peak discharge could reflect the role of peak discharge events in gravel scour (Holtby and Healey 1986) and the inverse relationship between peak discharge and gravel quality of the stream bed at the depth where coho salmon eggs incubate (Scrivener and Brownlee 1989).

COHO MODEL

sub-model	output=fn(inputs)	function output is affected by density dependence	 climate freshwater	 marine	 logging
1	fecundity = fn(female fork-length)				
	egg survival = fn(peak discharge)	○	●		○
	#emergent fry = fn(#females, fecundity, egg survival)				
2	date of fry emergence = fn(spring thermal summation)		●		●
3	#resident fry = fn(#emergent fry)	●	○		○
4	#fall fingerlings = fn(#resident fry)	●	○		○
5	fingerling size = fn(summer density, emergence timing)	●	●		●
6	winter survival = fn(fingerling size, habitat quality)	○	○		●
	probability of smolting = fn(fingerling size, habitat quality)		○		●
	#yearling smolts = fn(over-winter survival, prob. of smolting)				
	#residual yearlings = fn(over-winter survival, prob. of smolting)				
7	smolt weight = fn(fingerling size)	○	○		○
	residual size = fn(fingerling size)		○		○
8	#fall yearlings = fn(#residual yearlings)	●	○		○
	yearling size = fn(habitat quality)	○	○		●
9	#age 2 smolts = fn(#fall yearlings)	●	○		○
	smolt weight = fn(yearling size)	○	○		○
10	smolt migration timing =fn(April thermal summation)		●		●
11	smolt-to-adult survival = fn(smolt weight, migration timing)				
12	adjusted smolt-to-adult survival = fn(sea surface temperature, surface salinity, fishery rate)	○		●	
	#escapement = fn(#smolts, adjusted smolt survival)				

FIG. 3. Major components of the coho salmon population model. The important modifiers of each relationship are shown by a closed circle, where we detected the effect in this study, an open circle, where the effect has been detected elsewhere and may have been present in Carnation Creek, or no symbol, where no effect was expected or detected.

Sub-model 2 predicts the median emergence date of the fry from the Celsius thermal summations for February and March (CTS_{febmar}):

$$(14)\quad JD_{emerge}\ (Julian) = -0.272 \cdot CTS_{febmar} + 190.2,$$

$$(r=0.892,\ n=16,\ P<0.001).$$

Emergence timing is strongly correlated with late winter stream temperatures (Holtby 1988c; Scrivener and Andersen 1984).

Sub-model 3 predicts the number of fry that take-up residence in the stream shortly after emergence, N_{resid}, from N_{emerge}. A surprisingly large proportion of the fry that do emerge (~0.54) leave the stream very shortly after emergence. The relationship between the number of resident and emergent fry is described by a hyperbolic saturating function:

$$(15)\quad N_{resid} = 54556 \cdot .N_{emerge}/(70134+N_{emerge}),$$

$$(r=0.90,\ n=17,\ P<0.001).$$

The relationship indicates that Carnation Creek has an average carrying capacity for fry of ~28 000 or ~9 fry·m^{-1}. The carrying capacity imposes an upper limit on the number of resident fry. However, even with emergence considerably below that number significant numbers of fry leave the stream. Why they do so is unknown although there may be an adverse effect of freshets around the time of emergence (Scrivener and Andersen 1984).

Sub-model 4 predicts the number of fingerlings residing in the stream in the fall of their first year from the N_{resid}:

$$(16)\ N_{fall\ 1} = 17020 \cdot N_{resid}/(10530 + N_{resid}), \quad (r=0.872,\ n=15,\ P<0.01).$$

The observations suggest that Carnation Creek has an average carrying capacity in the fall of their first year of ~12 050 first-year fingerlings or ~4 fish·m^{-1}. This presumable habitat limitation was reached in 8 of the 15 years for which there are data (1971–86). Although there was some variation around this average number, we were unsuccessful in identifying a physical correlate of that variation. Logging had no detectable effect on carrying capacity measured over the entire stream but the addition of fine logging debris did temporarily increase carrying capacity in affected stream sections (Scrivener and Andersen 1984). Carrying capacity subsequently declined in those same sections after the debris was removed and the channel configuration changed by winter freshets.

Sub-model 5 predicts the average FL (mm) of fingerlings in the fall of their first year:

$$(17)\quad FL_{fall\ 1} = -0.254 \cdot JD_{emerge} - 0.0005 \cdot gmDensity + 91.7, \quad (r=0.912,\ n=16,\ P<0.001),$$

where gmDensity is the geometric mean density of sub-yearling coho over the summer, estimated from the observed densities in the first and third annual population estimates. The addition of densities of the older age class of coho and/or other species weakened the density dependent term, suggesting that interactions between sub-yearling coho and other age groups or species are relatively unimportant. Although summer growth rates did increase in some stream reaches immediately after logging (Scrivener and Andersen 1984), when averaged over all of the study sections, summer growth rates were not affected by logging, and in particular, were not affected by increased summer stream temperatures (Holtby 1988c).

Sub-model 6 predicts the number of yearling smolts ($N_{smolt\ 1}$) and the number of residual yearlings resident in the stream after the first winter ($N_{yearlings}$) by predicting $p_{winter\ survival}$, the probability that sub-yearling fingerlings survive the winter, and $p_{smolting}$, the probability that sub-yearlings surviving the winter would smolt:

$$(18)\quad p_{winter\ survival} = -1.188 + 0.0232 \cdot FL_{fall\ 1} + 0.288 \cdot HQI_w, \quad (r=0.897,\ n=17,\ P<0.001).$$

Most of the variability in winter survival was associated with changes in fish size going into the winter. Winter survivals were greatest when HQI_w signified large pool and debris volumes.

$$(19)\quad p_{smolting} = 0.425 + 0.0111 \cdot FL_{fall\ 1} - 0.478 \cdot HQI_w, \quad (r=0.898,\ n=17,\ P<0.001).$$

The proportion of sub-yearling fingerlings that smolted increased with the mean size of the fingerlings in the preceding fall, possibly a reflection of a size-threshold that must be obtained before smolting occurs. The proportion that smolted also increased as habitat quality fell. We suspect that as the quality of winter habitat in the main channel (indexed by HQI_w) fell after logging, an increasing proportion of smolt production was originating from the off-channel habitat on the valley floor. That habitat has been relatively little affected by logging (Hartman and Brown 1987). High growth rates obtained by fish exploiting those off-channel habitats (Brown 1985) further suggest that most of those fish smolted in the following spring. Although overall, over-winter survivals increased in the winters after logging, the small fish remaining in the main channel, presumably those that would not have smolted in their first year, suffered greater mortality due to habitat degradation in the main channel.

The number of yearling smolts was then calculated:

$$(20)\quad N_{smolt\ 1} = 0.5 \cdot p_{smolting} \cdot p_{survival} \cdot N_{fall\ 1}.$$

Only numbers of adult female coho were calculated. The conversion from total numbers to female numbers was done in the calculation of smolt numbers above, by multiplying by 0.5, i.e. by explicity assuming an equal sex ratio in the smolts. That assumption is supported by unpublished sampling data from the spring of 1987 from Mesachie Creek, a small stream on the east coast of Vancouver Island ($p_{female}=0.47$, $n=151$, $P>0.2$ for H_0: sex ratio=0.5; LBH unpubl. data) and by data obtained for coho juveniles during their first summer in the ocean ($p_{female}=0.47$–0.54; R. Kadowaki, Pac. Biol. Sta., Nanaimo, pers. comm.).

The number of residual yearlings was then calculated:

$$(21)\quad N_{yearlings} = (1 - p_{smolting}) \cdot p_{survival} \cdot N_{fall\ 1}.$$

Sub-model 7 predicts the weights of the yearling smolts and the FL of the residual yearlings.

$$(22)\ a.\quad FL_{smolt\ 1}(mm) = 0.738 \cdot FL_{fall} + 38.9, \quad (r=.837,\ n=17,\ P<0.001);$$

$$(23)\ b.\quad W_{smolt\ 1}(g) = 10^{(2.6 \cdot \log_{10} FL_{smolt\ 1} - 4.29)}, \quad (r=0.983,\ n=32,\ P<0.001);$$

(24) c. $FL_{yearlings}(mm) = 0.923 \cdot FL_{fall} + 17.7$,
$(r=0.832,\ n=16,\ P<0.001)$.

Both $FL_{smolt\ 1}$ and $FL_{yearlings}$ were simply related to the size of sub-yearlings in the preceding fall and we could not identify any additional physical or biological correlates.

Sub-model 8 predicts the number and size of yearlings in their second fall:

(25) a. $FL_{fall\ 2} = 2248 \cdot N_{yearlings}/(1117 + N^{yearlings})$,
$(r=0.846,\ n=17,\ P<0.001)$;

(26) b. $FL_{fall\ 2}\ (mm) = -20.1 \cdot HQI + 95.9$,
$(r=0.788,\ n=17,\ P<0.001)$.

The number of yearlings in the fall was an asymptotic function of the number present in the spring, suggesting that there was a carrying capacity for the yearlings of ~2050 or ~0.7·m^{-1}. Their length was a decreasing function of the habitat quality index. The sizes of yearling coho began to decrease after the beginning of logging in marked contrast with the sub-yearlings (sub-model 5), probably because of the loss of main-stem pool habitat that was observed after logging (Hartman et al. 1987). The differences in the response of sub-yearlings and yearlings probably reflect the different habitat requirements of the two age-groups (Bisson and Sedell 1984).

Sub-model 9 predicts the numbers and weights of the 2 yr-old smolts:

(27) a. $N_{smolt\ 2} = 0.5 \cdot 1194 \cdot N_{fall\ 2}/\ (465 \cdot N_{fall\ 2})$,
$(r=0.729,\ n=17,\ P<0.001)$;

(28) b. $FL_{smolt\ 2}\ (mm) = 0.468 \cdot FL_{fall\ 2} + 63.5$,
$(r=.544,\ n=17,\ P<0.05)$;

(29) c. $W_{smolt\ 2}\ (g) = 10^{(2.6 \cdot \log_{10} FL_{smolt\ 1} - 4.29)}$,
$(r=0.983,\ n=32,\ P<0.001)$.

The number of female smolts is predicted by multiplying the estimate of total smolt numbers by 0.5. The number of 2-yr-old smolts is an asymptotic function of the numbers of yearlings present in the fall, indicating a winter carrying capacity for 2-yr-old fish of ~1050 fish or ~0.3 · m^{-1}. The sizes of the 2-yr-old smolts were proportions of the sizes of the yearlings in the preceding fall. We were unable to identify any additional biological or physical correlates. Unlike the sub-yearlings, the over-winter survival of the yearlings was not correlated with the size at which they entered the winter. Interestingly the estimated average survival of yearlings, 0.645, is similar to the survivals of the largest of the sub-yearlings, suggesting that over-winter survival is an asymptotic function of size (Holtby 1988b).

Sub-model 10 predicts the median date of smolt emigration for both smolt age groups from the Celsius thermal summations for April:

(30) a. $JD_{smolt\ 1} = -0.109 \cdot CTS_{apr} + 149.5$,
$(r=.818,\ n=16,\ P<0.001)$;

(31) b. $JD_{smolt\ 2} = -0.135 \cdot CTS_{apr} + 154.7$,
$(r=.798,\ n=16,\ P<0.001)$.

Sub-model 11 predicts smolt survivals from smolt weights and median emigration dates using a time and size-at-release model for coho (model for y_1, Table 5 in Bilton et al. 1982). The general form of the model has been confirmed in other similar experiments (B. Morley, Pac. Biol. Sta., Nanaimo, B.C., pers. comm.). Total numbers of females surviving to a time immediately prior to the fishery were then calculated:

(32) $N_{pre\text{-}fishery\ 1} = \text{smolt survival} \cdot N_{smolts}$.

Sub-model 12 utilizes the time series of fishing mortality rates observed for the Robertson Creek coho and the observed returns to Carnation Creek to estimate $N_{pre\text{-}fishery\ 2}$. More than 90 % of the Robertson Creek fish that are caught are taken by the offshore troll fishery immediately off the west coast of Vancouver Island and many (~50 %) are reported caught in the statistical area which includes Barkley Sound. We assume that Carnation Creek fish were similarly exploited because adults of both stocks must follow similar return routes, they enter their natal streams during the same time period, and the troll fishery ends about one month prior to their return (Argue et al. 1987). The differences between the two estimates of $N_{pre\text{-}fishery}$ were expressed as residuals:

(33) $\text{residual} = N_{pre\text{-}fishery\ 2} - N_{pre\text{-}fishery\ 1}$.

This residual is presumed to result from variability in smolt survival that was not accounted for by changes in smolt weight and migration timing. We then sought correlates of the residuals from among a small set of measurements of ocean conditions: SST_{spring}, the average sea surface temperatures at Amphitrite Point for April–June of the years of smolt migration, SST_{winter}, the average sea surface temperatures at Amphitrite Point for October–February, the winter following smolt migration and $SSSA_{spring}$ and $SSSA_{winter}$, the salinity anomaly for the same periods measured at Amphitrite Point. The following models were computed with step-wise regression. For the yearling smolts;

(34) $\text{residual} = 271.54 - 28.45 \cdot SST_{winter} + 20.8 \cdot SSSA_{spring}$,
$(r=0.770,\ n=11,\ P<0.05)$;

and for the 2 yr-old smolts;

$$(35)\ \text{residual} = -9.51 \cdot SST_{winter} + 88.7, \quad (r=0.621,\ n=11,\ P<0.05).$$

When winter temperatures were cold and, for the yearling smolts, when spring salinities were high, the residuals were large and positive indicating that survivals were better than the Bilton estimates. Conversely, when winter temperatures were warm and salinities were low, survivals were poorer than Bilton estimates.

The escapement of adult female coho salmon to Carnation Creek was then calculated as follows:

$$(36)\ \text{Return} = \text{smolt survival} \cdot (1 - \text{fishing mortality}) \cdot N_{smolt} + \text{residual}.$$

When the observed time series of physical variables and numbers of spawners are used as inputs, the predicted returns of adult females agree reasonably well with those observed (Fig. 4). The model explains between 66 and 71 % of the variance in returns for each age class and for the total return. The slopes of the regressions of observed returns on predicted returns are in no case significantly different than 1.0 and the intercepts are in all three cases statistically indistinguishable from 0.0. In some years there were large discrepancies between the predicted and observed returns (e.g. 1979; Fig. 4). We attempted to establish where in the model sequence the discrepancies arose by substituting observed values of the outputs of the various submodels. The discrepancies in returns from both age-classes of smolts originate largely from errors in estimating the numbers of sub-yearling fish in the fall ($N_{fall\ 1}$). That error is the residual variation around the summer carrying capacity of the stream for which we could not identify any physical correlate.

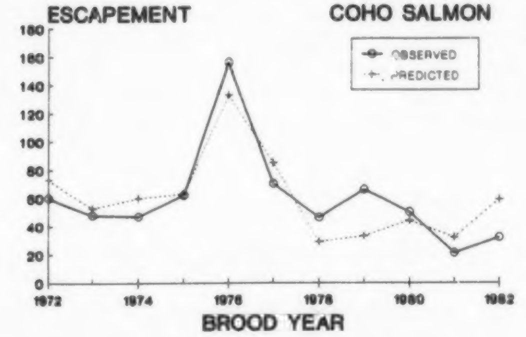

FIG. 4. Observed and predicted escapements of coho salmon adult females to Carnation Creek. Both age-groups were combined.

Results

Stock-Recruitment Relationships

By varying the number of spawners over a large range while holding all of the independent physical variables to some constant value, we calculated stock-recruitment relationships for both species (Fig. 5,6). We did this for three sets of conditions: average conditions observed before logging (brood years 1970–74); the same pre-logging conditions with stream temperatures set to the long-term average derived from Estevan Point air temperatures and average conditions observed after logging (1978–86). The two parameters, α and ß of the Ricker stock-recruitment relationship;

$$(37)\ \text{recruitment} = \alpha \cdot \text{stock} \cdot e^{-\beta \cdot \text{stock}}$$

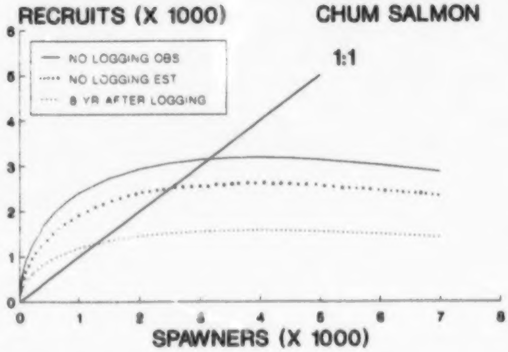

FIG. 5. Stock-recruitment relationships for the chum salmon of Carnation Creek estimated for observed pre-logging stream conditions, estimated long-term pre-logging stream conditions, and observed stream conditions 8 yr after logging.

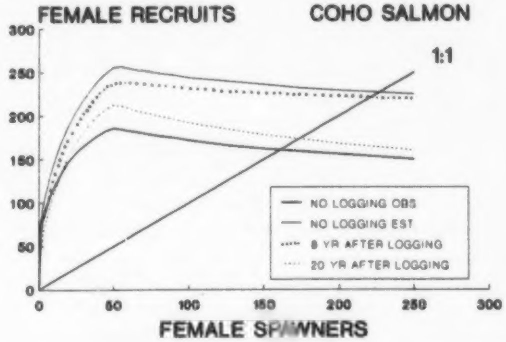

FIG. 6. Stock-recruitment relationships for the coho salmon of Carnation Creek estimated for observed pre-logging stream conditions, estimated long-term pre-logging stream conditions, observed stream conditions 8 yr after logging and estimated stream conditions 20 years after logging.

(Ricker 1975) were estimated using a non-linear parameter estimator (Wilkinson 1986).

For both species, the estimated values of α for the pre-logging scenarios (Table 2) are very similar to those derived for the region by Walters et al. (1982), while the estimated values of ß are considerably less. The differences in parameter values indicate that stock-recruitment curves fitted to the regional stock aggregates are more domed-shaped than are the fairly flat-topped curves fitted to the Carnation Creek data. The similarities in the values of α between Carnation Creek and the stock aggregates indicates that the shapes of the stock recruitment curves are similar below the levels of maximum recruitment. As a result of those similarities, the values of the important harvest parameters are very similar for the Carnation Creek stocks and the regional stock aggregates (Table 2).

The 52-yr average stream temperature is slightly warmer than the average temperature observed over the 4 years prior to logging. As indicated by the stock-recruitment analyses, higher stream temperatures have different effects on the two species. For chum salmon, productivities (recruits/spawner), equilibrium stock sizes, and sustainable exploitation rates were all lower at the higher temperatures (table 2), while the opposite was true for coho salmon.

Inter-Annual Climatic Variability

The length of the Carnation Creek study was too short to adequately characterize inter-annual variability in the climate. To some extent this has been demonstrated already in the stock-recruitment analyses where it was shown that water temperatures in the 5 years before logging were lower than the probable long-term average, resulting in greater stock productivity for chum salmon and the reverse for coho salmon (Table 2). In order to characterize inter-annual variability we felt that it was necessary to simulate recruitment over a longer period of time. To do so required time series of all of the independent physical variables. Time series of sea surface temperatures and salinity anomalies were available from 1934 to present (Dodimead 1984). A time series of water temperatures from 1934 to present was calculated using a relationship between monthly mean air temperatures at Estevan Point, B.C. and mean stream temperatures in Carnation Creek (Holtby 1988c). We were unable to find any predictive model for peak discharge. Instead we determined a frequency distribution for peak winter discharges for the nearby Somass River and used that distribution to simulate a time series of peak discharges that spanned the observed range at Carnation Creek (9–65 m^3·s^{-1}). For coho salmon fishing mortality was set to 67%, the 13-yr average. The relative contributions of freshwater and marine factors to inter-annual variability were estimated by holding one of the two sets of independent variables constant (median values), while allowing the other set to vary. The simulation of chum recruitment was begun with the 1934 brood year with 2300 spawners (pre-logging mean). The age and sex compositon of the spawners were held constant at the average values observed over the study period. For coho salmon, the simulation was begun in 1934 assuming 70 female spawners (pre-logging mean) equally divided between the two age-groups.

TABLE 2. Estimated Ricker stock-recruitment parameters for the Carnation Creek chum salmon and coho salmon stocks. α and ß are the parameters of the Ricker stock-recruitment relationship. S is the number of spawners, R/S is the number of recruits per spawner, μ is the exploitation rate. In the "observed" scenarios, observed values of the physical variables were used in the simulations, while in the pre-logging "estimated" scenarios, average stream temperatures derived from a simulated time series of stream temperature from 1934 to present were used. Parameter estimates for NWVCI (north-west Vancouver Island) were derived from data presented in Walters et al. (1982).

scenario	α	ß	max. recruitment		max. sustained yield		
			S	R/S	S	R/S	μ
CHUM							
pre-logging: observed	3.031	0.0003	3145	1.115	1482	1.892	0.471
estimated	2.475	0.0003	3145	0.910	1252	1.662	0.398
northwest VCI	3.217	0.0445	—	1.183	—	1.967	0.492
post-logging: observed	1.497	0.0003	3145	0.551	601	1.236	0.191
COHO							
pre-logging: observed	5.973	0.0100	100	2.197	67	3.050	0.672
estimated	7.350	0.0087	115	2.704	83	3.576	0.720
northwest VCI	8.585	0.210	—	3.158	—	4.044	0.753
post-logging: observed	6.502	0.0101	122	2.392	85	3.253	0.693

Comparisons of the simulated recruitment with estimates of the total stock sizes from brood years 1947–74 for chum salmon and brood years 1958–77 for coho salmon (Walters et al. 1982) indicate that our simulation has captured the important components of inter-annual variability in both chum (Fig. 7) and coho salmon (Fig. 8). Regressions of the smoothed and standardized time series for the combined stocks of northwest Vancouver Island (NWVCI) on the smoothed Carnation Creek time series (SCC) confirm the similarity between the observed and simulated time series:

$$(38)\ \text{chum: NWVCI} = 0.611(\text{SCC}) - 158.0, \quad (r{=}0.39,\ n{=}27,\ P{<}0.05);$$

$$(39)\ \text{coho: NWVCI} = 0.908(\text{SCC}) - 16.8, \quad (r{=}0.47,\ n{=}20,\ P{<}0.05).$$

However, the predicted levels of inter-annual variability in both coho and chum salmon are lower than those observed in the NWVCI stock aggregate (Table 3).

Inter-annual variability in chum numbers appears to

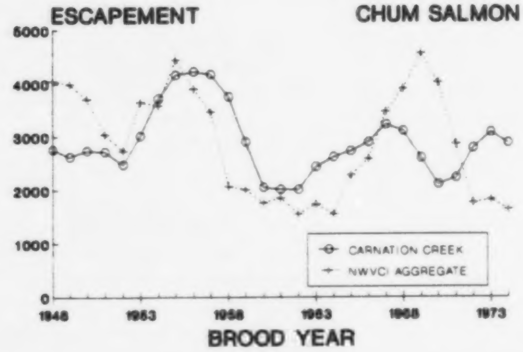

FIG. 7. Comparison of the simulated escapement time series for Carnation Creek chum salmon and the northwest Vancouver Island stock aggregate over the period 1947–74 (brood years). The data have been smoothed using a 3-year running average. The mean of the stock aggregate was scaled to the mean of the Carnation Creek stock. Adults were assumed to mature at age 4.

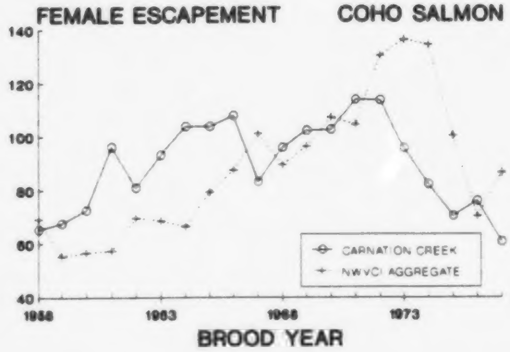

FIG. 8. Comparison of the simulated escapement time series for Carnation Creek coho salmon and the north-west Vancouver Island stock aggregate over the period 1958–77 (brood years). The data have been smoothed using a 3-year running average. The mean of the stock aggregate was scaled to the mean of the Carnation Creek stock.

TABLE 3. Partitioning "natural" variability between freshwater and marine factors. Model simulations were run for 48 years under three scenarios: (1) both freshwater and marine factors varied simultaneously, (2) freshwater factors were fixed at median values and, (3) marine factors were fixed at median values. Variability in escapement for each of the simulations is summarized as the inter-quartile range, the range between the 12.5 and 87.5 percentiles encompassing 75 % of the observations, the total range and the percentage coefficient of variation (%CV). The numbers in brackets are the proportions that the ranges were of the overall median stock size, 2653 for chum and 93 for coho. Values for the north-west Vancouver Island stock aggregates (NWVCI) are from Walters et al. (1982).

Measure of escapement variability	Marine & freshwater		Freshwater		Marine		NWCI	
CHUM								
range: 25–75 %	1169	(0.44)	744	(0.28)	781	(0.20)	—	(0.63)
range: 12.5–87.5 %	1521	(0.57)	1069	(0.40)	1670	(0.41)	—	(1.14)
total range	2987	(1.13)	2194	(0.83)	2454	(0.69)	—	(1.59)
%CV	26 %		18 %		22 %		39 %	
COHO								
range: 25–75 %	45	(0.48)	27	(0.29)	33	(0.36)	—	(0.83)
range: 12.5–87.5 %	80	(0.86)	44	(0.47)	57	(0.69)	—	(1.44)
total range	141	(1.52)	64	(0.69)	108	(1.16)	—	(2.02)
%CV	34 %		20 %		26 %		50 %	

be equally attributable to variation in freshwater and marine factors (Table 3). The variability itself must arise largely in the ocean however, since one of the important freshwater factors, spring temperatures, does not affect survival in freshwater but affects the survival of the fry shortly after they have entered the ocean. Inter-annual variability in coho numbers also originates both in freshwater and, to a slightly greater extent, in the ocean (Table 3).

Logging Effects

Logging effects were estimated in three ways. First, stock recruitment relationships for both species were generated using the models and average values of the physical variables observed in the 8-yr period after logging (1978–86).

Second, the average effects of logging over the same period were estimated directly by estimating mean recruitment had logging not occurred (Rec_{nolog}) and comparing those estimates with mean estimated recruitment for the period after logging (Rec_{after}):

$$(40)\quad \%\text{logging effect} = 100\,\% \cdot (Rec_{after} - Rec_{nolog})/Rec_{nolog}.$$

Expected stream temperatures without logging were estimated using the stream temperature model of Holtby (1988c). Mean particle sizes of the stream-bed (D_g) and the habitat quality index (HQI) were set to pre-logging averages. All other physical variables were as observed. The relative contributions of logging-related changes in the physical variables affected by logging were estimated by fixing all but one of the variables to the value that would have been observed had logging not occurred.

Third, the effects of logging were estimated over a longer time period by simulating clear-cut logging of 40 % of the watershed at various times during the 48-yr period for which we had time series of the physical variables. Temperature time series after logging were simulated using the temperature model of Holtby (1988c). We assumed that the full temperature effect lasted for 5 yr after logging followed by a linear reduction in the temperature effect that concluded with temperatures returning to pre-logging levels 15-yr after forest harvest. A hypothetical time series for HQI was constructed by assuming that full recovery after logging takes 50 yr. For a 3-yr period after logging, the index increased from a pre-logging value of 0.89, to 1.0 reflecting the addition of logging debris to the stream. During the next 8-yr period the index declined linearly to 0.3. The values of the index during this time conform closely to observed changes in stream conditions between 1976 and 1986. During the last 39-yr period, the index increased linearly from 0.3 to the pre-logging value of 0.89. Values of HQI were assumed the same during summer and winter. A 50-yr recover path may have been too short, and our assumption of full recovery after that time optimistic. However, other research does indicate that a total 50-yr time span of changes after logging is reasonable (Grette 1985). Alternative recovery paths, that assumed either longer periods for recovery or only partial recovery, did not substantially change our results, probably because of the relatively minor role that HQI played in determining levels of variability in production of coho salmon adults. Peak discharges were assumed unaffected by logging (Hetherington 1982). The simulated harvest differed from the actual logging treatment that was conducted in that we assumed that 40 % of the watershed was clear-cut in a single year rather than over a 5-yr period. Our simulated harvest resulted in immediate changes to spring temperatures and gravel quality rather than the gradual changes that were actually observed and consequently the full effects of logging on stream conditions appeared immediately.

The three approaches indicated that the two species were affected by logging but that the magnitudes and timing of the effects were different for each species. The stock recruitment analysis (Table 2) indicated that logging had a considerable and damaging effect on chum salmon: at the level of maximum sustained yield (MSY), equilibrium abundance and sustainable exploitation rates were halved and recruits per spawner was reduced by 50 % of the observed pre-logging value. The response of coho salmon to logging was similar to their response to higher stream temperatures: at MSY, individual productivity, sustainable exploitation rates and equilibrium stock sizes were slightly larger.

In our direct measure of logging effects, chum salmon escapements were reduced by an average of −24.9 % (Table 4), while for coho salmon, logging produced a small decrease in escapements that averaged −5.9 % (Table 5). The decrease in chum salmon escapements resulted from earlier fry migration that was associated with increased spring temperatures and from poorer incubation survivals associated with increases of fines in the spawning gravels (Table 4). For coho salmon, the temperature changes observed after logging were associated with a 3.6 % decrease in escapements (Table 5). Further partitioning the temperature effect indicated that earlier fry emergence associated with increased temperatures during February and March was associated with an increase of 23.3 % in escapements while earlier smolt emigration associated with increased temperatures in April was associated with a decrease of 31.8 %. Note that the temperature effects are not additive because of the non-linearities embodied in several of the sub-models. The reductions in habitat quality that were observed after logging reduced escapements by 8.4 %.

TABLE 4. Calculation of the average effect of logging on chum salmon recruitment. The time series of predicted total recruitment are "logging" where all variables were as observed after logging, "no-logging" where both spring temperatures and mean particle size of the gravel were set to probable values assuming no logging, "gravel=NL" where only mean particle sizes were set to pre-logging values, and "temp.=NL" where only spring temperatures were set to pre-logging values. Only brood years affected by logging are shown.

	Predicted total recruitment			
Brood year	Logging	No-logging	Gravel=NL	Temp.=NL
1975	1904	1643	1888	1657
1976	2091	3011	2502	2517
1977	1993	2425	1821	2653
1978	2327	3316	2931	2632
1979	1232	1691	1531	1360
1980	1117	1993	1117	1993
1981	1874	2219	1940	2144
1982	626	1236	876	882
Average effect of logging	—	−24.9%	−9.9%	−16.9%

TABLE 5. Calculation of the average effect of logging on coho salmon escapement. Predicted female escapements are denoted "logging" where all variables were as observed after logging, "no-logging" where both spring temperatures and mean particle size of the gravel were set to probable values assuming no logging, "temp=NL" where only stream temperatures were set to pre-logging values and "HQI=NL" where the habitat quality index was set to pre-logging values. Only brood years affected by logging are shown.

	Predicted escapements			
Brood year	Logging	No-logging	Temp.=NL	HQI=NL
1975	63	72	72	63
1976	121	119	118	122
1977	63	55	55	64
1978	23	24	22	25
1979	52	46	43	37
1980	35	52	49	71
1981	21	18	15	15
1982	65	68	69	69
Average effect of logging	—	−5.9%	−3.6%	−8.4%

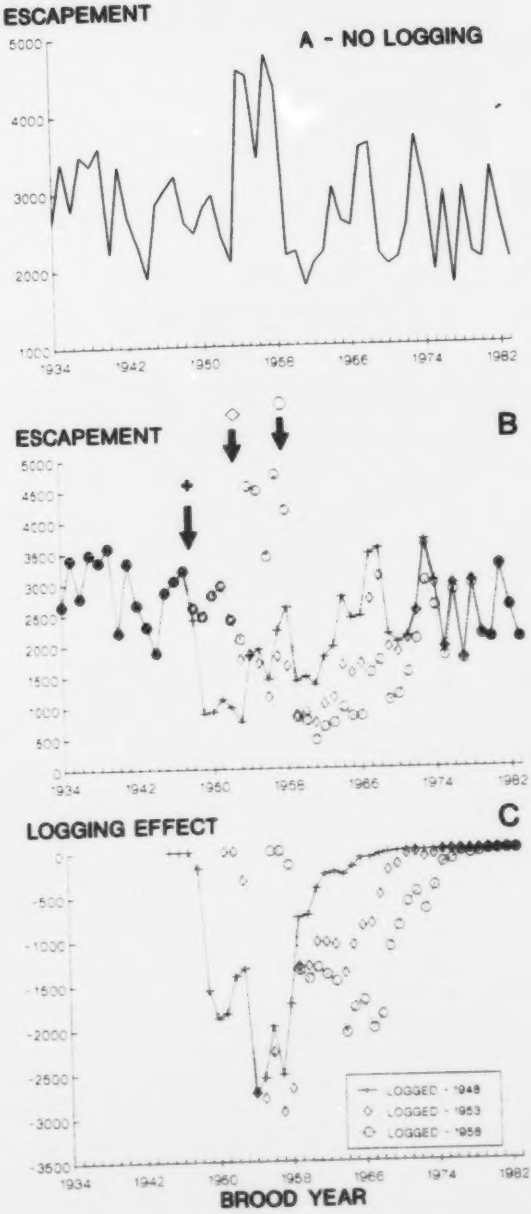

FIG. 9. Simulated chum escapements with three episodes of logging. (A) Escapement without logging. (B) Escapement with forest harvest indicated by arrows. (C) Effect of logging on escapement equal to difference in escapements after logging (B) and escapement without logging (A).

The effects of logging demonstrated in the long-term simulations were substantially different from the preceding analyses. For chum salmon, the predicted effects of logging averaged over the ten years following forest harvest were 55% to 69% reductions in stock size compared to the long-term median stock size (Fig. 9). The predicted effects of logging were much greater than those estimated in the preceding analyses. The greater impacts predicted by our simulation probably result from the application of a one-time forest harvest and the resulting acceleration of effects.

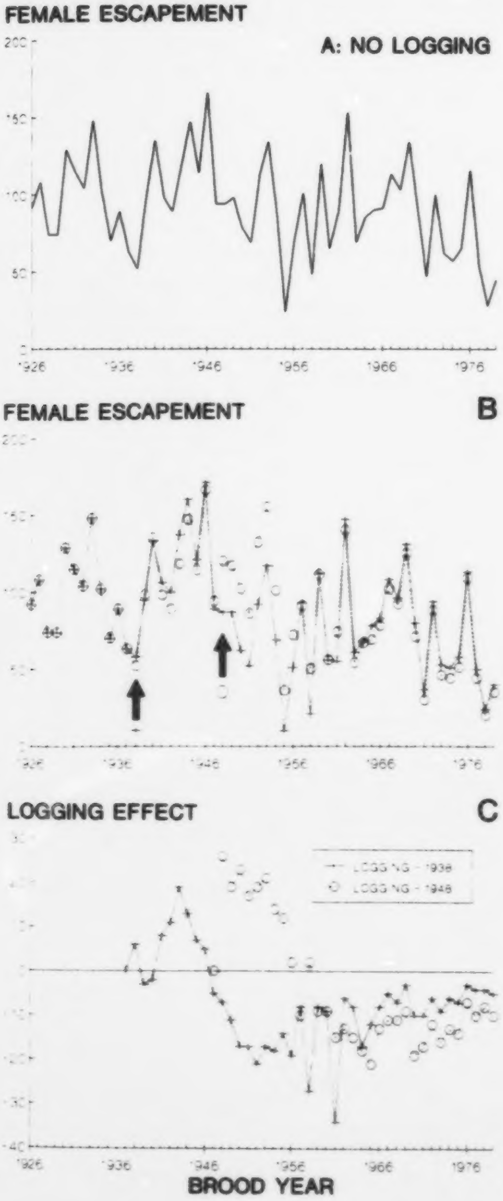

FIG. 10. Simulated coho escapements with two episodes of logging. (A) Escapement without logging. (B) Escapement with forest harvest indicated by arrows. (C) Effect of logging on escapement equal to difference in escapements after logging (B) and escapement without logging (A).

For coho salmon, the time series of logging effects produced by these simulations (Fig. 10) show a 9-yr period of increased escapements followed by 30 yr or more of decreased escapements. For four simulations with logging occurring in 1931, 1936, 1941 and 1951, the increases in escapements over the first 5 years ranged from 6.1 to 23.8 %. The logging effect averaged over the first 30 years ranged from 0 % to a 7.1 % decrease.

For both species, the effect of forest harvest depended on the year in which logging occurred (Fig. 9,10). If forest harvest occurs during a downward phase of the productivity cycle then the average decrease in stock size is greater than if forest harvest occurs during the upward phase. Logging at Carnation Creek occurred during an upward phase of the productivity cycle (Holtby 1988c).

Fishing Mortality

In most years there was no fishery on the chum salmon, other than a small native food fishery off the stream mouth. In contrast, the coho salmon were affected by the substantial troll fishery off the west coast of Vancouver Island. We used the simulation models to estimate the effect of the fishery on inter-annual variability. First, we examined population responses to fishery exploitation which had uniform, random distributions over probable ranges for each species; 0–0.5 for chum and 0.59–0.80 for coho. For chum salmon, the time series with random fisheries are similar to escapement time series calculated with a constant fishery, with correlation coefficients ranging between 0.77–0.90. For coho salmon the time series with random and fixed fisheries are nearly identical with correlation coefficients ranging between 0.90–0.96. For both species, the patterns of variability in adult numbers that arose from climatic variation were little changed by realistic variations in fishing mortality. Furthermore the overall levels of variability remained unchanged, with the coefficient of variation increasing from 26 % to 33 % for chum salmon and decreasing from 40 to 36 % for coho salmon. That result supports the hypothesis of Wooster (1984) that variability in fishing pressure is not an important contributor to inter-annual variability in fish abundance.

Second, we examined changes in the levels of variability with directed rather than random changes in average fishing mortality. For both species we expected levels of variability to increase with increasing fishing mortality since increased mortality would eventually reduce the number of spawners to the point where density-dependent compensatory mechanisms would saturate and buffering against environmental variation would be reduced. The expected behavior was produced by the models for both species (Fig. 11).

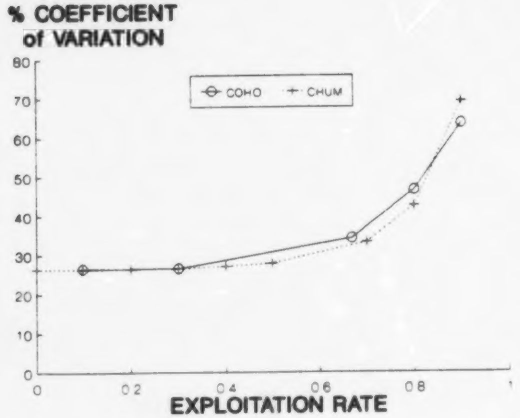

FIG. 11. Variability in escapements of chum and coho salmon as a function of fishery exploitation rate.

Discussion

The two species of Pacific salmon found in Carnation Creek responded differently to natural and anthropogenic variability in their rearing environments. Fluctuations in adult abundance that could be ascribed to climatic variability were lower in chum salmon than in coho salmon and while chum salmon were affected roughly equally by variation in freshwater and marine conditions, coho salmon were slightly more sensitive to variability in the ocean. Chum salmon were considerably more susceptible to the effects of habitat alteration than were coho salmon. However, the predicted levels of variability in adult abundance of both species are considerably lower than observed variability in marine species such as herring (Cushing 1975).

Some of our results seem contrary to conventional expectations about the sources of inter-annual variability in the numbers of the two species. Intuitively, coho salmon should be more susceptible than chum salmon to variations in the freshwater environment because of their longer residency there. Conversely, coho salmon enter the ocean at a much larger size than chum salmon do and spend less time there, and should be less sensitive to variability in ocean conditions. Chum salmon should be less sensitive to logging disturbances than coho salmon, also because of their much shorter residency in freshwaters. Neither of these expectations is supported by our results. Variability in both species was associated roughly equally with variability in freshwater and marine conditions. Coho salmon appear slightly more responsive to variability in ocean conditions than do chum salmon. Logging 41 % of the watershed was associated with a short-term increase in the abundance of coho salmon but had little effect on the coho population when averaged over a 30-yr period. In contrast, logging significantly reduced the abundance and productivity of the chum salmon.

For both species variations in the timing of life history events was an important source of variability in adult numbers. Most of the effects of logging and climatic variability in freshwaters were expressed through temperature-related changes in the timing of fry emergence and smolt emigration. The critical temperature changes, occurring in the late winter and spring, were generally small, and were common to both species. The associated variability in the timing of fry emergence and smolt emigration had surprisingly large consequences for adult abundance. Further research into the mechanisms that underlie the apparent importance of migration timing is clearly warranted.

The apparent importance of the timing of life history events suggests that both species of salmon found in Carnation Creek are adapted to the local thermal regime. The importance of the timing of life history events and therefore, the importance of local adaptations to thermal regimes might be general characteristics of salmon populations (Leggett and Carscadden 1978; Tallman 1986; Walters et al. 1978). If so the maintenance of adaptations to local conditions should be of considerable concern not only in any manipulation of fish stocks for the purposes of stock rebuilding or enhancement but also when other activities in a watershed, forest harvest for instance, threaten the viability of a stock. In particular, it may not be wise to attempt to rebuild runs using fish that originated from systems with different thermal regimes.

The variability in smolt survival of both species was associated with variability in sea surface temperatures and salinities in Barkley Sound during the first few months after smolt migration. Furthermore, the directions of those associations were the same for both species: warm temperatures and low salinities were associated with poor survivals. Sockeye salmon stocks in Barkley Sound are apparently similarly affected by local oceanic conditions (K. D. Hyatt, Pacific Biological Station, Nanaimo, B. C., pers. comm.). We think it unlikely that smolt survival was directly linked to changes in physical conditions in the ocean but, instead, was related to changes in the distribution, abundances or activities of predators over the continental shelf off the west coast of Vancouver Island. Entry into the ocean is a time of high mortality for both chum salmon fry (Healey 1982) and coho salmon smolts (Matthews and Buckley 1976). The distributions and feeding habits of two potential predators, mackerel (*Scomber japonicus*, and hake (*Merluccius productus*) are currently being studied in the Barkley Sound area (D. Ware, Pacific Biol. Sta., Nanaimo, B.C., pers. comm.). Both of those species are predators of salmon smolts and both are present off-shore and to the south of Barkley Sound. During the recent periods of high sea surface temperatures and low salinities both species became abundant in Barkley Sound and near the shore to the north of the Sound (Fulton and LeBrasseur 1985). Reductions in available food or changes in the community of food organisms during those same periods of warm water intrusion could have reduced the growth rates of salmon fry and smolts and increased the period of time that they were susceptible to predation. Alternatively, unusual oceanic conditions could have affected the abundance or distribution of other forage fishes in the region, leading to increased predation on juvenile salmon by piscivorous fishes and birds. In either case, the largest determinant of intra-annual variability for both species of salmon would have been variability in predation, itself driven by responses of the predators to climatic variability (Sissenwine 1984b).

The response of both species, but particularly chum salmon, to a habitat disturbance was dependent on the timing of the disturbance relative to "natural" variability. That dependence would make it difficult to ascertain the real effects of a habitat disturbance by simply monitoring abundance at any life stage, but particularly adults or smolts, since the effects of the habitat disturbance are confounded with the effects of natural variability (Pella and Myren 1974). The modeling approach that we employed enabled us to estimate the effects of logging since we explicitly controlled for climatic variability.

Variability in adult abundance of both species increased with increasing fishing mortality. At high (but not unrealistically so) levels of exploitation, variability in adult abundance was 2–3 times greater than at moderate levels of exploitation. The coincidence of severe habitat disturbance, adverse oceanic conditions and sustained high exploitation would lead to increased levels of variability at reduced abundances for both species. Such co-incidences may underlie the current crises in Strait of Georgia chinook and coho salmon stocks. For chum salmon which were considerably affected by habitat disturbance, such a coincidence of stresses could lead to such severe depression of numbers that no exploitation would be possible for considerable periods of time. Only limited exploitation of chum salmon stocks in Barkley Sound has been permitted since 1962, following a collapse in the stocks in that year. That collapse may have been the culmination of excessive exploitation in the preceding 12 years (Lightly et al. 1985), the occurrence 3.5 yr earlier of a 2-yr period of high ocean temperatures and low salinities (Fulton and LeBrasseur 1985) and extensive logging of many major watersheds in the area between 1945 and 1960 (Brown et al. 1987).

Acknowledgments

We thank the many people who have participated in the Carnation Creek study over the years and especially B. C. Andersen who is largely responsible for the continuity and quality of the information used in our modeling. P. A. Bisson, K V. Koski, K. D. Hyatt, and B. E. Riddell critically reviewed the manuscript and provided many useful comments.

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Juvenile Salmonid Responses to Log Storage in Littoral Habitats of the Fraser River Estuary and Babine Lake

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Abstract

LEVY, D. A., T. G. NORTHCOTE, K. J. HALL, AND I. YESAKI. 1989. Juvenile salmonid responses to log storage in littoral habitats of the Fraser River Estuary and Babine Lake, p. 82–91. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Juvenile salmon often pass through and reside in littoral habitats of estuaries and lakes on their downstream migration to the Pacific Ocean. These migrants can be exposed to stored log booms and log-related habitat modifications. Effects of log storage on juvenile salmon were evaluated in two contrasting littoral storage areas. In the Fraser River estuary, juvenile chinook and chum salmon densities were similar in an area intensively utilized for log storage and in an adjacent marsh. Epibenthic invertebrates were abundant throughout the storage area. In Babine Lake, juvenile sockeye salmon were not observed in a recently-developed log transportation facility that became severely hypoxic during the vernal warming period. Deoxygenation was the result of an elevated biochemical oxygen demand produced by a microbial gelatinous slime layer which coated the underside of floating logs. Benthic insect larvae in the storage area were drastically reduced by the deposition of gelatinous slime material and wood debris. The contrasting results from the two studies probably reflected differences in water exchange processes in the log storage sites. Where water circulation is restricted, severe degradation of water quality may influence the littoral distribution of juvenile salmon.

Résumé

LEVY, D. A., T. G. NORTHCOTE, K. J. HALL, AND I. YESAKI. 1989. Juvenile salmonid responses to log storage in littoral habitats of the Fraser River Estuary and Babine Lake, p. 82–91. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Dans bon nombre de cas, des saumons juvéniles traversent les habitats littoraux dans les estuaires et les lacs et y font halte au cours de leur dévalaison vers l'océan Pacifique. Ces migrateurs peuvent être exposés à des estacades flottantes ou à des habitats dégradés par la présence de billes. Les effets du stockage des billes sur les saumons juvéniles ont été évalués dans deux zones littorales où des méthodes de stockage distinctes étaient employées. Dans l'estuaire du fleuve Fraver, les densités des saumons quinnats et kétas juvéniles étaient similaires dans une zone servant de façon intensive au stockage des billes et dans un marais adjacent. Les invertébrés épibenthiques étaient abondants dans l'ensemble de l'aire de stockage. Dans le lac Babine, aucun saumon rouge juvénile n'a été observé dans une installation de transport des billes récemment aménagée, où les conditions étaient fortement hypoxiques au cours de la période de réchauffement vernale. Une désoxygénation a été provoquée par une demande biochimique en oxygène élevée due à une pellicule microbienne gélatineuse recouvrant le dessous des billes flottantes. Le nombrede larves d'insectes benthiques dans la zone de stockage a diminué, de façon marquée, par suite du rejet de matières biologiques gélatineuses et de débris de bois. Les résultats des deux études reflétaient probablement des différences à l'égard des processus d'échange d'eau dans les aires de stockage des billes. Lorsque la circulation d'eau est entravée, une forte dégradation de la qualité de celle-ci peut influer sur la répartition littorale des saumons juvéniles.

Introduction

Juvenile Pacific salmon in their migration from inland rearing areas to oceanic feeding areas often pass through littoral estuarine habitats. Some species of juvenile salmon reside temporarily in these areas at least for several days and in some cases for up to several months (Reimers 1973; Dunford 1975; Healey 1979,1980; Levy and Northcote 1982). Likewise in lakes young sockeye salmon entering from tributary or outlet river emergence areas may spend an initial period of time in littoral residence before moving offshore into their limnetic rearing areas (McDonald 1969).

Temporary residence by young salmon in shallow littoral habitats of estuaries and lakes, as productive as these can be, also may bring the hazards of vulnerability to the many human industrial activities which occur in such regions. Perhaps for some of the same reasons that young salmon take shelter in littoral habitats, it is convenient and often less costly for forestry operations to temporarily store large numbers of logs in these protected waters. Consequently it is not surprising that in recent years there has been much study and review of the utilization and needs of juvenile salmon in littoral habitats of estuaries and lakes in relation to log storage (Pease 1974; Dorcey et al. 1978; Sibert and Harpham 1979; Waldichuk 1979; Anon. 1980; Duval et al. 1980; Levy et al. 1982; Levy and Hall 1985; Sedell and Duval 1985).

The lower Fraser River and especially the area around the mouth of its North Arm (Fig. 1) encompasses what is surely one of the largest and most concentrated log storage areas in North America, covering approximately 1500 ha (Fraser River Harbour Commission, Vancouver, B.C., unpublished data). Through this general area pass, and to varying degrees reside, the largest overall populations of juvenile salmon to be found anywhere in the world (Northcote and Larkin 1989) with total numbers exceeding 300 million on some years. Babine Lake is the largest natural inland water body entirely within British Columbia and supports the major stocks of sockeye salmon coming from the Skeena River, the second largest river system in the province. Although major logging activities have been conducted in the watersheds of Babine Lake and its tributaries since the 1950's, a recent operation has resulted in the temporary storage of some 166 000 m^3 of logs in a bay within Morrison Arm (Fig. 1), close to the point where several million young sockeye fry enter each year from upriver spawning grounds. These same logs eventually are towed down the arm and across the lake to be held again temporarily at a dewatering site not far from the Fulton River mouth where annually up to several hundred million young

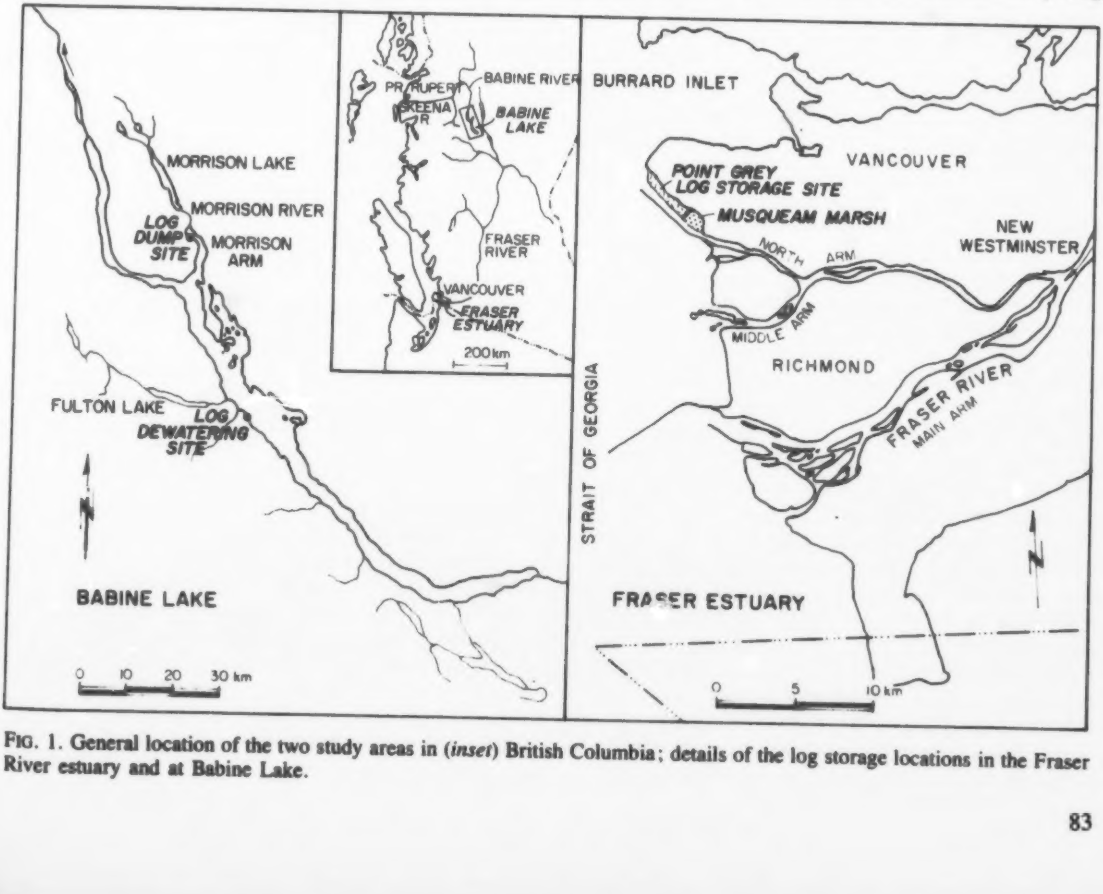
MORRISON LAKE
MORRISON RIVER
LOG DUMP SITE
MORRISON ARM
FULTON LAKE
LOG DEWATERING SITE
BABINE LAKE
0 10 20 30 km
PR. RUPERT
SKEENA R
BABINE RIVER
BABINE LAKE
FRASER RIVER
VANCOUVER
FRASER ESTUARY
200 km
BURRARD INLET
VANCOUVER
POINT GREY LOG STORAGE SITE
MUSQUEAM MARSH
NORTH ARM
NEW WESTMINSTER
MIDDLE ARM
RICHMOND
FRASER RIVER MAIN ARM
STRAIT OF GEORGIA
FRASER ESTUARY
0 5 10 km

FIG. 1. General location of the two study areas in (*inset*) British Columbia; details of the log storage locations in the Fraser River estuary and at Babine Lake.

sockeye enter the lake from a large artificial spawning channel. Even closer to this site is another log dewatering operation handling some 100 000 - 200 000 m^3 of logs each year.

Because of the occurrence of large numbers of both juvenile salmon and logs in these two very different littoral habitats – estuarine and lake – it would seem useful to review some aspects of our recent studies there and to make comparisons between them with a view towards understanding the functional interactions involved and the possibilities of minimizing damages to the salmon stocks concerned. Furthermore, in the estuarine study, we were fortunate in being able to utilize a large-scale habitat manipulation "experiment" resulting from recent closure of a portion of the log storage area on Musqueam Marsh (details of the history of usage are presented in Levy et al. 1982). We then compared this regenerating marsh with an adjacent area still being heavily affected by log storage. Also at the Babine Lake log storage site we had detailed water quality and biological data both from a localized area of dense over-winter storage as well as from nearby areas with no log storage. Information was collected during the year prior to, as well as in the two successive years following the start of log storage.

Methods

Sampling in the Fraser estuary

Between May and July of 1980, juvenile salmon populations in the Point Grey log storage area were compared with those in the adjacent Musqueam Marsh (Fig. 1). Sampling sites were established in dendritic tidal channels that drain the marshes and mudflats of the Fraser estuary. Tidal channels chosen for study had mouth widths and lengths of approximately 10 m × 400 m, respectively (Fig. 2). Sampling within tidal channels was undertaken by fishing a 0.6 cm mesh beach seine as an intertidal trap net (Levy and Northcote 1982). At high slack tide, a 2.4 m × 15 m net was fastened to stakes driven into the tidal channel banks. As the tide ebbed over a 5–7 h period, detritus and plant debris was removed so that they continued to filter effectively. At low tide, the fish entrained in a shallow pool upstream of the trap were seined into a small section of the net, and then transferred into a 10 % formaldehyde solution for subsequent enumeration and laboratory analysis. Previous gear efficiency tests conducted with marked juvenile salmon elsewhere in the Fraser estuary (Levy and Northcote 1982) indicated that the samplers operated with an efficiency of about 50 %, effectively capturing about half of the tidal channel fish population upstream of the trap net.

During mid-May of 1981, fish samples were obtained from tidal channels in the Musqueam Marsh and the Point Grey log storage area and quantified by estimating the volumetric discharge through the trap nets at the time of sampling. At 30–min intervals between high and low tide, water depths were estimated both at the sides and in the middle of the tidal channels with a measuring pole in order to calculate the sampling cross-sectional area of the trap net. Surface flow rates were measured with a Model 201 Marsh–McBirney electromagnetic current meter attached to a wading rod. Water discharge estimates were obtained by averaging the flow rates over a 30–min period and multiplying by the mean cross-sectional area of the channel during the same interval. These estimates were summed over the period between high and low tide when the trap nets were operating to provide a measure of the volumetric discharge through the samplers.

A predominant epibenthic invertebrate in the Musqueam Marsh and the Point Grey log storage area, the amphipod *Eogammarus confervicolus*, was sampled in basket traps (Levings 1976). Baskets were constructed from 1.8 cm mesh netting material sewn into a 20 × 40 cm bag. The traps were loosely stuffed with approximately 1 kg wet weight of washed *Fucus* obtained from a nearby marine intertidal area (English Bay) at low tide. Traps were suspended in tidal channels for a 1–2 w period, and after removal frozen in a plastic bag prior to laboratory analysis. In the laboratory, organisms in the traps were identified and counted, and the dry weight of alga determined after drying at 100°c for 48 h.

Sampling in Babine Lake

Previous investigations at Babine Lake (McDonald 1969) have shown that upon entering the lake, juvenile sockeye reside for one month in the littoral zone before shifting offshore for the remainder of their one (occasionally two) year lake occupancy. Sampling during the present study focussed on the residency of juvenile sockeye in the littoral zone where they would be potentially vulnerable to near-shore log storage impacts. Relative densities of juvenile sockeye in the log dump site in Morrison Arm (Fig. 1) and in neighboring reference areas were obtained by visual observation. Counting grids (1 m × 1 m) were established with wooden pegs and string at a distance of 1 m from the shoreline. Observers stationed atop adjacent 2 m stepladders counted the number of sockeye fry swimming through the grids over a 15–min period. The few fish which back-tracked were counted every time they passed through the grid during the counting period.

Field measurements of temperature and dissolved oxygen were undertaken in the log dump site with a regularly calibrated YSI Model 54 dissolved oxygen meter. Vertical *in situ* measurements were made at 1 m intervals from surface to bottom at 5 sampling locations (Fig. 6) on 5 dates extending between May 30 and June 21, 1985.

The chemical oxygen demand (COD) was determined by the dichromate reflex method (American Public Health Association et al. 1985). Bacteria were enumerated by the acridine orange direct count epifluorescence technique as modified by Daley and Hobbie (1975). The counts were made under oil immersion with a Leitz Ortholux microscope and cell volume was determined by dimension measurements with the microscope micrometer. Cell volumes were converted to carbon using a factor of 5.6×10^{-13}g carbon•μm^{-3} (Bratback 1985).

Larval stages of terrestrial insects predominate in the benthos of Babine Lake (Yesaki and Levy 1986). Consequently we evaluated log storage-induced changes in the benthic insect community by dredging. A minimum of 3 replicate Ekman dredge (520 cm^2 in 1983; 230 cm^2 in 1984 and 1985) samples were washed in a 0.34 mm mesh seive and then preserved in 10 % formalin. In the laboratory, organisms were separated from detritus, identified to genus or species and then counted.

Results

Fraser Estuary

There were similar population densities of chinook, chum, and pink salmon fry and threespine sticklebacks in Fraser estuary tidal channels of the regenerating marsh and the log storage area during the spring and early summer of 1980 (Fig. 2). On most sampling

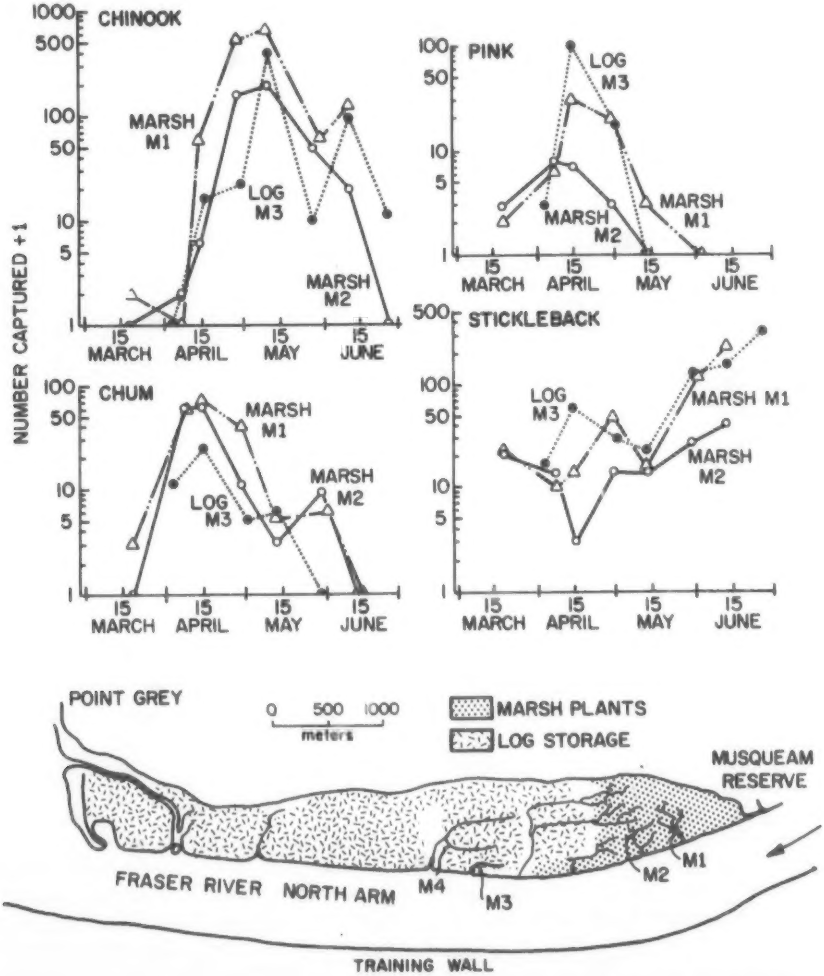

FIG. 2. Seasonal changes (1980) in tidal channel trap net catches of salmon fry and sticklebacks at a log storage (M3) and regenerating marsh sites (M1, M2) on the North Arm of the Fraser River estuary.

dates, fish catches at the log storage site (M3) were similar to those obtained at the marsh sites (M1, M2). Quantitative comparisons of fish densities in tidal channels of Musqueam Marsh and the Point Grey log storage area were undertaken in May of 1981 (Fig. 3). Differences between the 2 areas were tested by two-way analysis of variance (unequal but proportional subclass numbers as described by Sokal and Rohlf (1981)) and found to be non-significant ($F_{1,12}$= 0.07). These results provide quantitative evidence for similar fish population densities in tidal channels of the Musqueam Marsh and the Point Grey log storage area.

The gammarid amphipod *E. confervicolus*, a commonly occurring prey in the diet of juvenile salmon in estuaries (Levings 1976), was the most frequently occurring invertebrate in the basket traps. Smaller numbers of isopods *Gnorimosphaeroma oregonensis* and tube-dwelling amphipods *Corophium* sp. were also captured; detailed results are presented elsewhere (Levy et al. 1982). The abundance of *E. confervicolus* did not appear to be greatly influenced by the presence of log booms (Fig. 4). On one sampling series (July 8–15, 1980) higher numbers of gammarids were trapped in baskets positioned in the log storage sites (two-level nested ANOVA results: $F_{1,8}$= 7.804, $0.05 > P > 0.01$). The higher density of amphipods in the log storage area during 1980 may have been related to a salinity gradient running through the study area (Levy et al. 1982). In the two other 1981 sampling series (Fig. 4), numbers of amphipods trapped were similar in the log storage and marsh sites.

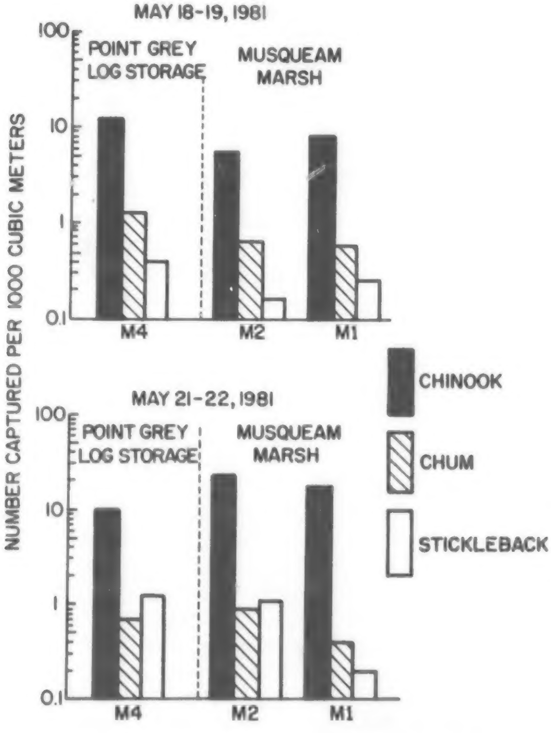

FIG. 3. Mid-season (1981) densities (numbers per unit volume) of salmon fry and sticklebacks in waters draining log storage and regenerating marsh sites on the North Arm of the Fraser River estuary.

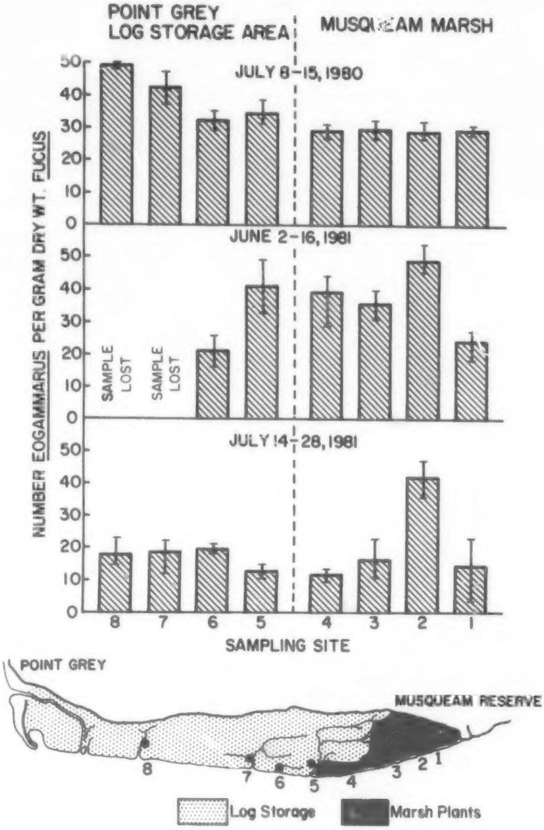

FIG. 4. Relative abundance of gammarid amphipods (*Eogammarus confervicolus*) in eight study areas during three experimental periods. Histograms show the mean and bars show the range of 2 samples for 1980, and 4 samples for 1981.

Babine Lake

Juvenile sockeye were present in littoral habitats of Morrison Arm for several weeks in May of 1983 and 1985, both prior to and after the start of log transportation. The distribution pattern of juvenile sockeye salmon in the littoral zone was markedly altered on 2 sampling dates in 1985 (Fig. 5). On May 21, sockeye fry were present in the log dump site, and numbers observed in counting grids were similar to those observed at reference sites. On May 27, however, sock-

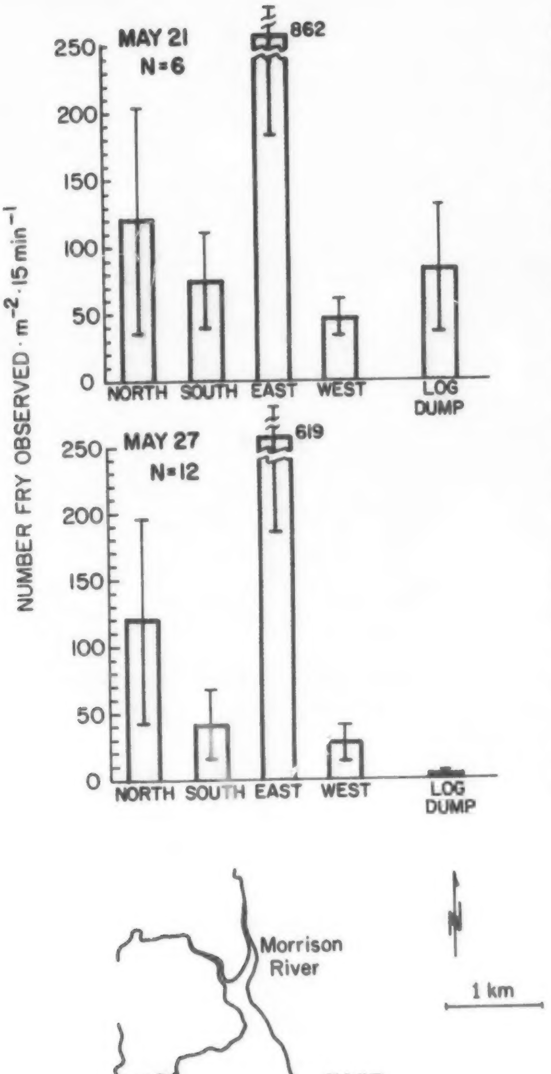

FIG. 5. Mean number of sockeye fry passing littoral counting grids in Morrison Arm of Babine Lake on two dates in May, 1985. N indicates sample size and bars represent 95 % confidence interval.

eye fry were relatively sparse in the dump site and only 2 fry•m^{-2}•15 min^{-1} were observed in log dump site grids (Fig. 5). One-way analysis of variance of the observation grid data (transformed to (no. fry observed + 1)$^{1/2}$) gave a non-significant F value on May 21 ($F_{1,29}=0.34$; probability >0.05) and a significant value on May 27 ($F_{1,59}=5.70$; probability $= 0.019$). The difference in results reflects the low numbers of sockeye fry in the log dump site on May 27.

Juvenile sockeye likely avoided the log dump site in response to a severe reduction in the dissolved oxygen concentration. The first data collected at the log dump site (2 m station) for water quality conditions (15 May, 1985) after ice-out on 12 May, 1985 showed a slight depletion with surface values close to 8 mg•L^{-1} (80 % saturation). On 27 May, these waters were becoming more depleted in oxygen with surface values close to 5 mg•L^{-1} (55 % saturation) and by 30 May severe oxygen depletion was recorded at numerous sampling stations (Fig. 6). Several sites had surface dissolved oxygen concentrations below 1 mg•L^{-1}. The zone of low dissolved oxygen persisted through the month of June (Fig. 6), although the areal coverage and severity decreased, probably in response to changes in water temperature and wave turbulence.

Hypoxic conditions within the log dump site apparently resulted from bacterial respiration and growth which was stimulated by organic carbon leachates from the floating logs. Estimates of microbial biomass and chemical oxygen demand indicated elevated values in the epilimnion of the log dump site (Fig. 7). The bacteria were also present on the underside of submerged logs and formed a gelatinous slime mat 1–3 cm in thickness. Thick strands of bacterial slime (maximum 0.5 m length) could be observed hanging beneath log bundles during SCUBA dives made in May of 1985. The slime material occasionally sloughed off the log bundles, and coated bottom sediments within the log dump site.

Unlike the log dump site, there was no evidence of water quality changes within the log dewatering site, and epilimnetic dissolved oxygen values remained close to 100 % saturation. The log dewatering site is exposed to considerable wind and wave turbulence and physical mixing processes tend to counteract log storage-induced water quality changes.

Benthic insect larvae, largely diptera, ephemeroptera, and trichoptera, were severely decreased by log storage (Fig. 8). In both the log dump site and the log dewatering site, decreases in abundance corresponded to the start-up of transportation activities. Insect larvae were largely absent from affected areas of the log dump site in June of 1984, and remained low in abundance through August 1985 (Fig. 8). In the log dewatering site, insect larvae decreased following log transportation start-up, and then re-appeared in large numbers in August 1985 (Fig. 8). The re-appearance reflected high numbers of one species, *Chironomus decorus*, which

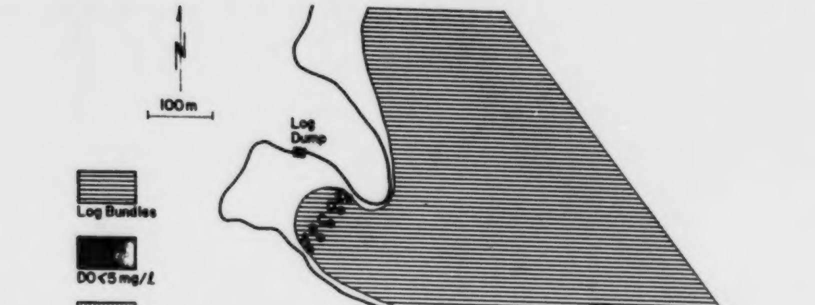

FIG. 6. Dissolved oxygen and temperature isopleths for a transect through the log dump site in Morrison Arm on 5 dates between late May and June, 1985.

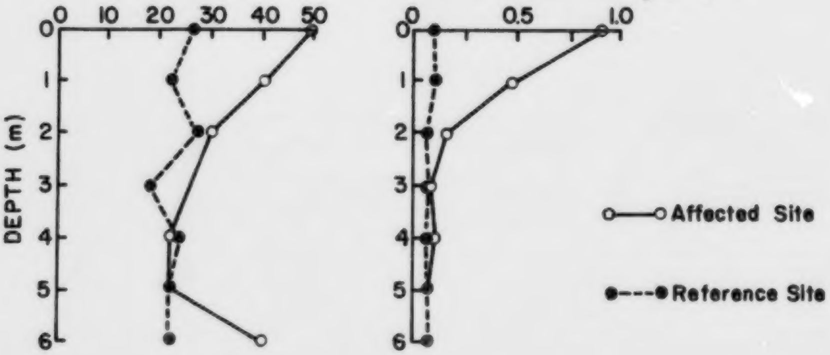

FIG. 7. Vertical profiles of chemical oxygen demand (COD) and bacterial biomass at affected (C on FIG. 6) and reference (southwest of log booming area) sites on June 6,1985.

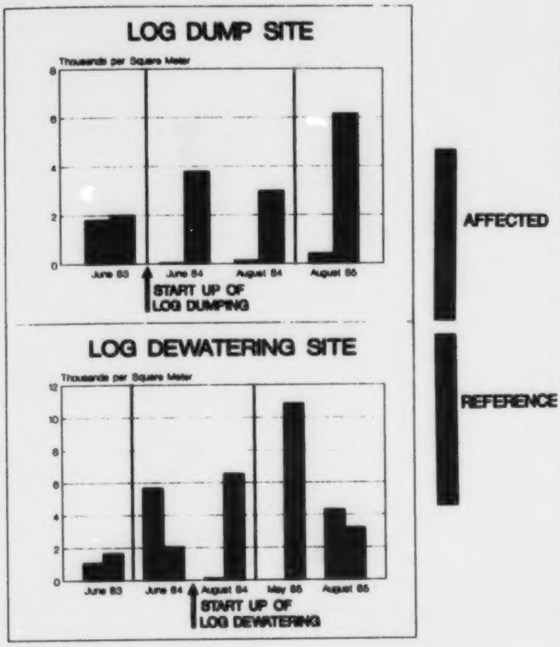

FIG. 8. Mean benthic insect larvae densities in the log dump and log dewatering sites between 1983 and 1985.

was evidently tolerant of the altered benthic environment.

Discussion

The similarity in fish catches from the tidal channels of the log storage area and the regenerating marsh along the North Arm of the Fraser River estuary suggest that the seasonal timing and relative abundance of juvenile salmon in the two regions do not differ greatly. Also for one period during concentrated seasonal utilization, no significant difference in salmon fry or stickleback densities could be demonstrated between the areas. These observations suggest that log storage has neutral or minimal effects on juvenile salmon utilization of the Point Grey log storage area.

Log storage could indirectly affect fish growth and survival in the Fraser estuary if impacts were evident on invertebrate food organisms. However, our epibenthic trap data (Fig. 4) indicate that such is not the case for at least one important estuarine amphipod. Other estuarine crustaceans, including the mysid *Neomysis mercedis*, were more numerous in the log storage area than the adjacent marsh (Levy et al. 1982) and the log storage area appears to support a substantial production of crustacean invertebrates. The most striking and consistent difference between prey utilized by young salmon feeding in the different tidal channels was a shift from insects, which were dominant in the diet of those from the regenerating marsh, to epibenthic macroinvertebrates in the log storage site (Levy et al. 1982). This shift may result from complex differences in relative abundance and availability of prey between the sites. Although the methods we used to sample invertebrate prey in the channels were not effective for insects (especially those in surface drift), we frequently observed adult chironomid swarms in association with *Scirpus* and *Carex* macrophyte stands as well as many adults on the surface drift of dewatering marsh tidal channels. These were rarely seen in the log storage tidal channels in which emergent macrophyte stands are virtually absent. In spite of the reduced insect abundance in the log storage area, there was no evidence of higher proportions of empty stomachs or reduced amount of food in fish from such sites (Levy et al. 1982).

The log dump site studied at Babine Lake was in a rather protected bay off a narrow arm of the main lake and therefore was subject to reduced wind-driven circulation of water. The area was covered with a large volume of recently cut logs, and severe oxygen depletion rapidly developed shortly after the ice cover had melted. Young sockeye fry entering the arm avoided the shoreline in the oxygen depleted bay, as evidenced by the grid count data. During *in situ* bioassay studies conducted in the affected area on 3 June 1985, sockeye fry exhibited severe respiratory distress and suffered 100% mortality within a 15-min exposure (Power 1987). Since we never observed moribund or dead fry in the deoxygenated water, we suspect that sockeye avoided the area through either a vertical or horizontal habitat shift. Avoidance of deoxygenated water is a common response of fish to hypoxic stress (Kramer 1987).

Davis (1975) reviewed the oxygen requirements of fish and used the incipient oxygen response threshold, the oxygen concentration at which physiological, biochemical and behavioral responses are evident, for establishing dissolved oxygen criteria in natural waters. The average incipient oxygen response threshold for freshwater salmonids ($n = 19$ studies) was 6.00 $mg \bullet L^{-1}$ at 15°C. At dissolved oxygen concentrations of 4.16 $mg \bullet L^{-1}$ it was inferred that a large portion of freshwater salmonids would be affected by hypoxia. During the present study, surface dissolved oxygen concentrations were frequently less than 2 $mg \bullet L^{-1}$, well below safe levels, and probably representing lethal conditions for sockeye salmon at the ambient temperatures of the log dump site.

Juvenile sockeye are largely planktivorous in Babine Lake and exploit both copepods and cladocerans as a food source. In addition to crustacean zooplankton, sockeye fry acquire larval insects as a secondary food source while in the littoral zone (Levy et al. 1985). Benthic insect larvae were rapidily and drastically depleted both in the log dump site and the dewatering site, probably due to the deposition of gelatinous slime material and log debris which sloughed off the log booms. The implications of a reduction in benthos for juvenile sockeye growth and survival rates are difficult to evaluate quantitatively. However, if juvenile sockeye are "food-limited" in littoral habitats, as they are in the limnetic zone (Brett 1983), then log storage could have an impact on their feeding and growth rates, and ultimately upon their survival. Foerster (1954) presents mark-recapture evidence which indicates that sockeye marine survival rates are positively correlated to smolt size at the time of downstream migration.

Some major differences were evident in the responses of juvenile salmon to log storage in littoral habitats of the two major study areas – the Fraser River estuary and Babine Lake. In the former, along the outer margin of a river arm, the habitat was subject to continual water exchange by river current as well as diurnal tidal flushing. Due to the high volume of water exchange, hypoxic conditions would be unlikely to persist in Fraser estuary log storage areas, although oxygen values below saturation have been recorded in some deeper midchannel pockets of the North Arm (Benedict et al. 1973) as well as in some slough habitats (Malick et al. 1985). In the log dump site at Babine Lake, severe oxygen depletion developed in the spring during a period of rapid epilimnetic warming shortly after the ice cover left, and persisted for over three weeks with surface concentrations that could quickly kill sockeye fry. Limited water circulation and mixing in the bay probably contributed to the severity and maintenance of such low oxygen levels. Tidal action in the Fraser estuary, while promoting increased water exchange, may well have had unfavorable consequences by destroying emergent macrophyte stands and compacting bottom sediments through the movement of fluctuating log booms in the intertidal region.

In freshwater lakes, especially those frequented by salmonids, a reduction in dissolved oxygen is an undesirable consequence of log storage. This habitat effect could be avoided by locating log transportation facilities in well-flushed littoral areas that experience moderate wind and wave turbulence. Removal of floating log booms immediately after the spring thaw, and prior to epilimnetic warming, would also minimize the possibility of log storage-induced hypoxia.

Evaluation of the impact of log storage on adult salmon production is confounded by intensive fisheries exploitation of the affected stocks. Due to the geographical location of the log dump site in Babine Lake, the Morrison River sockeye stock is potentially the most susceptible to habitat alterations resulting from recent log storage. This sockeye population overlaps in adult run timing through the commercial fishery with the much larger enhanced stocks produced in the Fulton and Pinkut Rivers (Smith and Jordan 1973) and in consequence, may be exposed to overharvesting. Most juvenile chinook salmon in the Fraser River estuary are believed to originate in the Harrison River (Levy and Northcote 1981). These same fish, while potentially vulnerable to industrial development within the Fraser estuary, are also heavily exploited in numerous coastal and freshwater fisheries. It therefore remains a challenging and difficult research question to distinguish the effects of a local nursery habitat impact from exploitation effects on the adult stock.

Acknowledgments

We wish to thank a large number of UBC students who participated in various aspects of the research including R. Barr, R.Chandler, B.Christensen, D.Hallson, A.Hooper, R.Northcote, B.Radford, C.Wyatt and L.Yamanaka. Assistance in chemical analysis and bacterial enumeration was provided by P.Wentzell. A.Dorcey of Westwater provided invaluble administrative support during all phases of the work. Funding for the Fraser estuary study was jointly provided by the Dep. of Fisheries and Oceans, the Canadian National Sportsmen's Fund, and the Council of Forest Industries. The Babine Lake study was funded under Section 88.2 of the B.C.Forest Act through a grant from Houston Forest Products Ltd. to the Westwater Research Centre.

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Habitat Alteration and Changes in Abundance of Coho (*Oncorhynchus kisutch*) and Chinook (*O. tshawytscha*) Salmon in Oregon's Coastal Streams

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Abstract

LICHATOWICH, J. A. 1989. Habitat alteration and changes in abundance of coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) in Oregon's coastal streams, p. 92–99. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Settlement and resource exploitation began altering fishery habitat in Oregon coastal streams in the mid-1800's, several decades before catch was recorded and nearly 100 years before the habitat or the fishery resource was inventoried. Timber harvest and agriculture were the principal activities leading to altered fishery habitats. Alteration of habitat increased after 1910 as mechanized technology came into general use in resource exploitation. Annual production of coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon about 1900 was 1 385 000 and 305 000 fish, respectively, compared with current production potential of 767 000 coho and 482 000 chinook salmon. I speculate that the apparent reduced abundance of coho salmon reflects the difference between coho habitat that was largely in pristine condition around 1900 and the existing, altered habitat. The apparent increase in abundance of chinook salmon may reflect the early destruction of habitats favored by chinook salmon before fishery data were available prior to 1900 followed by the gradual recovery of their habitat and of the chinook salmon populations. Alternatively, the increase in abundance of chinook salmon abundance may be the result of a shift from pristine habitats which favored production of coho salmon to the present altered habitat which favors production of chinook salmon.

Résumé

LICHATOWICH, J. A. 1989. Habitat alteration and changes in abundance of coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) in Oregon's coastal streams, p. 92–99. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

L'établissement et l'exploitation des ressources ont commencé à dégrader les habitats des poissons dans les cours d'eau côtiers de l'État de l'Oregon au milieu des années 1800, plusieurs décennies avant que l'on tienne des registres des captures et près de 100 ans avant que l'on fasse l'inventaire des habitats ou des ressources halieutiques. La récolte de bois d'œuvre et l'agriculture constituaient les principales activités qui se sont ainsi répercutées sur les habitats des poissons. La dégradation de ceux-ci s'est accélérée après 1910, au moment où, de façon générale, l'exploitation des ressources a été mécanisée. La production annuelle de saumons cohos (*Oncorhynchus kisutch*) et de saumons quinnats (*O. tshawytscha*) vers 1900 était respectivement de 1 385 000 et de 305 000 individus, alors que le potentiel de production actuel est de 767 000 saumons cohos et 482 000 saumons quinnats. Je présume que la réduction apparente de l'abondance des cohos est due à l'état de leurs habitats qui, vers 1900, étaient, dans une large mesure, intouchés, et qui sont actuellement dégradés. En ce qui concerne les saumons quinnats, l'augmentation apparente de leur abondance est peut-être une conséquence de la destruction des habitats qu'ils affectionnaient avant 1900, période pour laquelle nous ne disposons d'aucune donnée sur les pêches, suivie d'une remise en état progressive de ce refuges et de la reconstitution graduelle des populations de cette espèce. L'accroissement de l'abondance des quinnats peut aussi être dû à la transformation des habitats en bon état du début du siècle, qui favorisaient la production des cohos, en zones, actuellement dégradées, favorisant la production des quinnats.

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Introduction

As early as 1852, visitors observed sawdust and debris from logging and milling operations covering the sea as far as 30 miles off the mouth of the Columbia River (Swan 1977). We can only speculate as to the conditions in the streams from which the debris originated because these first changes in fish habitat preceded catch records by several decades and preceded inventories of the habitat and of the fishery resource by nearly 100 years. Chapman (1986) estimated predevelopment production of salmon (*Oncorhynchus* spp.) and steelhead (*Salmo gairdneri*) in the Columbia Basin to be from 7.4 to 8.9 million adult fish. Sedell and Luchessa (1981) and Johnson (1984) described the predevelopment condition of rivers in Oregon and tried to reconstruct the process by which fish habitat was changed into its present state. Sedell's work with Luchessa and Swanson (Sedell and Luchessa 1981; Sedell and Swanson 1984), in particular, has given resource managers new insight into what constitutes pristine salmon habitat and has caused resource agencies to reevaluate habitat restoration programs and the role of large woody debris in stream ecology. The early landings of coho, *O. kisutch*, and chinook, *O. tshawytscha*, salmon from coastal rivers were summarized by Cleaver (1951) and Mullen (1981a). But, since the work of McKernan et al. (1950) there has been no attempt to assess changes in salmon abundance resulting from freshwater habitat alterations.

Estimating historical production through an analysis of catch records is a judgmental process and will always be a subject of debate (Northwest Power Planning Council 1986). However, with the recent growth in programs to restore fishery habitat (Northwest Power Planning Council 1984; Bureau of Land Management 1985), a review of the historical record would help establish valid goals for restoration programs, and stimulate questions about habitat and fish production from a perspective that is different from site specific habitat evaluations. The purpose of this paper is to estimate changes in the natural production of Oregon's coastal stocks of coho and chinook salmon since the early 1900's and to speculate about the role of habitat in those changes.

Historical Overview of Habitat Losses

Logging

Early logging practices were particularly harmful to fish habitat in specific, local areas because trees were cut and the logs skidded near the streams, rarely more than a mile from a source of riverine transport (Holbrock 1956). Splash dams were used to aid the movement of logs downstream, a process that scoured the stream channel, removed spawning gravel, and cleared the stream of natural debris. At least 160 splash dams were in use in Oregon between 1880 and 1910 (Sedell and Luchessa 1981).

After 1910, steam "donkeys," spar poles, and high-lead rigging for logging operations and steam locomotives for log transport came into general use (Johansen and Gates 1957) so that more of the watersheds, particularly the steeper slopes, were exposed to timber harvest (Holbrock 1956). Lumber production grew rapidly after 1910, and, by 1938, Oregon was the nation's leading producer. Production increased through the 1940's then levelled off in the 1950's (Wall 1972). Logging on the steeper slopes increased sediment loads, raised stream temperatures, and promoted land slides and debris torrents (Bottom et al. 1985). By the 1950's, biologists had data to demonstrate relationships between timber harvest and declining salmon production in some coastal streams (McKernan et al. 1950).

After an intensive 15-yr study that documented the physical changes in stream habitats and the adverse effects of those changes on salmon and trout (*Salmo* spp.) populations (Moring and Lantz 1975), the Oregon legislature enacted the *Forest Practices Act* to protect fish habitats. Unfortunately, legislation has not solved all habitat problems associated with logging (Bradbury et al. 1986). For example, of 740 landslides in the Smith and lower Umpqua rivers in the winter of 1981–82, 5.5% were from natural causes and 94.5% were located in clear-cuts or were related to road building (Bottom et al. 1985).

Agriculture

The first irrigation projects began watering farmland in the 1840's. Cattle production, particularly in the eastern portion of the state, grew rapidly through the 1890's (Northwest Power Planning Council 1986).

In the coastal basins, irrigation developed later, after the 1920's, and primarily in the southern basins. Water diversion structures for irrigation (and power production) can have severe adverse effects on fish populations and once built and operating are difficult to correct. For example, Savage Rapids Dam on the Rogue River was built in 1921 to divert water to the Grants Pass Irrigation District. Fish losses at the project were first observed in 1928, but it took another 30 yr of study and negotiation before fish screens were installed (Pitney 1972). The installation of fish screens at Savage Rapids Dam and at two other diversions in the Rogue River increased total recruitment of adult spring chinook in the Rogue River by 30 000 fish over the pre-screening period (Lichatowich 1980).

Agriculture was probably not as destructive to coastal fish habitat prior to 1900 as the lumber and mining industries. Through the late 1800's agriculture did not grow as fast as other industries. Between 1880 and

1890, for example, the contribution made by farming to Oregon's wealth actually dropped from 50 to 27 % (Johansen and Gates 1957).

Hydropower

Although main stem dams cause important losses of adult and juvenile salmonids in the Columbia Basin (Thompson 1976), in coastal basins, less than 1 % of the total miles of historically usable streams have been made inaccessible to fish by dams (Pacific Fisheries Management Council 1979).

Mining

Gold was discovered in the John Day (Columbia Basin) and Rogue rivers in the 1840's and 1850's. Gravel bars were the most accessible sources of gold and were the first to be mined (Johansen and Gates 1957). Dredges stripped gravel from large sections of certain rivers. In addition, mining greatly increased sediment loads downstream from the actual mining site (Johnson 1984). The adverse effects of gold mining in coastal streams were concentrated in the Rogue Basin.

Numerical Changes in Coastal Stocks of Chinook and Coho Salmon

Methods

Historical catch estimates of coho and chinook salmon were compiled by Cleaver (1951) and Mullen (1981a). I shall assume that the production potential of Oregon's coastal streams for coho and chinook salmon at the turn of the century was represented by the average of the five highest catch years between 1893 and 1920 divided by an estimate of the harvest rate. I used peak catch years rather than five consecutive years during peak periods (Chapman 1986) to avoid including years when catch may have been reduced because of market conditions (Johnson 1983) independent of the abundance of salmon. The average catch of coho salmon for the peak years 1892, 1899, 1910, 1911, and 1915 was 554 000 (range 786 000 to 477 000) fish and the average catch of chinook salmon for the peak catch years of 1896, 1905, 1906, 1916, and 1917 was 122 000 (range 108 000 to 138 000) fish (Table 1).

Prior to 1923, catch statistics were derived only from the pack of canned salmon. As a result, total catch was underestimated by the amount of salmon landed, sold or kept for personal consumption without being processed through a commercial cannery. In 1901, 94 % of the total Oregon catch was canned, but by 1923 the proportion dropped to 32 % (Mullen 1981b). Because chinook salmon, particularly spring chinook, were favored by packers for canning (Gharrett and Hodges 1950), the proportion of chinook salmon canned probably remained high. Most of the noncanned product — frozen, mild cured, smoked, or pickled salmon — was produced from the catch of Columbia River salmon while a larger proportion of the coastal catch was canned (Cobb 1911). Unfortunately, data on the proportion of the coastal catch canned in the years between 1902 and 1922, which could be used to correct the catch estimates, are not available. Therefore, the catch data I used produced conservative estimates of production.

The harvest rates of coho and chinook salmon in coastal rivers were not measured until the 1950's, after restrictions on harvest had become effective (Gharrett and Hodges 1950) (Table 2). I therefore chose to assume a harvest rate of 40 % when estimating total production of coho and chinook salmon (Table 1). Under this set of assumptions, total production of coho salmon near the turn of the century was nearly 1.38 million fish and total production of chinook salmon was 305 000 fish (Table 1).

Chapman (1986) used catch data and optimal harvest rates reported in the literature (50–67 %) to estimate predevelopment production of salmon and steelhead in the Columbia River. A harvest rate of 40 % seems a reasonable assumption for the coastal fishery given the conditions and available evidence. The fishing industry on the Columbia River was well developed by the turn of the century, and harvest rates may have been at the optimum or even higher. Coastal fisheries of Oregon developed later. In 1880, Oregon's coastal fisheries

TABLE 1. Estimated abundance near the turn of the century and the current production potential (1 000's) of coastal coho and chinook salmon stocks from Oregon's coastal rivers.

Species	Average peak catches (1892–1920)	Assumed harvest rate	Assumed historical abundance (A)	Current production potential (B)	Difference (B–A)
Coho salmon	554	40 %	1 385	767[a]	−618
Chinook salmon	122	40 %	305	482[b]	+177

[a] From Oregon Department of Fish and Wildlife (1982).

[b] Modified from McGie (1982a and 1982b) and Cramer and Boyce (1986).

TABLE 2. Estimated exploitation rates for coho and for chinook salmon by commercial fisheries in Oregon coastal rivers.

Species, River	Year	Estimated exploitation rate (percent)	Source
Coho Salmon:			
Alsea	1951	15	Morgan and Cleaver (1954)
Tillamook Bay	1951	32	Willis (1954)
Nehalem	1952	29	Henry (1955)
Tillamook Bay	1953	29	Henry (1964)
Siletz	1954	12	Morgan (1964)
Chinook Salmon:			
Tillamook Bay	1953	36	Henry (1964)
Siletz	1954	36	Morgan (1964)

supported 2 canneries employing 95 persons compared with 29 canneries employing 4 000 persons on the Columbia River. By 1910, 5 634 fishermen were employed on the Columbia River, whereas 1 256 fishermen were employed in all of Oregon's coastal rivers. The number of canneries on the coast had, however, grown to 13.

The number of men employed in the early salmon fisheries may give a misleading impression of fishing effort relative to today's fisheries. Fishing in Oregon's coastal streams prior to 1920 was labor intensive. Early photographs show as many as 14 men working a beach seine (Smith 1979). A review of early records suggests that seining crews and the gill-netters had to spend a significant part of their time clearing snags from fishing sites, and weather and flow conditions seem continuously to reduce the catch (Hume 1909). In addition, fishermen were hampered by dependence on sail or rowing until they began converting to gasoline engines about 1915 (Smith 1979).

I estimated the current production potential of coastal rivers for coho and chinook salmon from stock-recruitment models instead of from catch data to reduce the influence of overharvest (underescapement) on recruitment and the influence of hatchery fish in mixed stock fisheries (Table 3). For example, total recruitment from natural reproduction of coho salmon in Oregon's coastal streams was estimated to be 230 000 fish in 1986 (Pacific Fisheries Management Council 1987), which is much less than either the estimated maximum recruitment or estimated recruitment at MSY (Table 3). In 1983, the parent year for the 1986 returns, coastal stocks were overharvested, and spawning escapement was only 57 200 fish or about 25 % of the 200 000 fish needed to meet escapement goals (Pacific Fisheries Management Council 1987). In recent years, hatchery fish have comprised 75 % of the catch of coho salmon (Oregon Department of Fish and Wildlife 1982).

To estimate current production of chinook salmon, maximum recruitment of coastal fall chinook stocks, Rogue River spring chinook, and Umpqua River spring chinook were summed (Table 3). The Rogue and Umpqua are the only major spring chinook stocks on the coast. The use of stock-recruitment models to estimate current production includes some risks. Errors in estimating harvest fraction or the number of spawners, lack of information on age or sex composition, or environmental "noise" can influence the reliability of parameter estimates (Risenbichler 1986). However, recruitment at low stock densities ($\hat{\alpha}$) from the stock-recruitment models used in this analysis (Table 3), appears to agree with estimates of ($\hat{\alpha}$) from stock-recruitment analyses of other salmon stocks in the Pacific Northwest and listed in Risenbichler (1986).

TABLE 3. Stock-recruitment relationships used to estimate current production potential of coastal coho and chinook salmon. α = Recruitment at low stock density; MSY = Maximum sustained yield.

Stock	Year-classes	α	Maximum recruitment (1 000)	Recruitment at MSY (1 000)
Coastal coho salmon[a]	1950–68	6.8	767	725
Coastal fall chinook salmon[b]	1953–75	9.9	370	360
Umpqua spring chinook salmon[c]	1964–77	6.8	20	19
Rogue spring chinook salmon[d]	1960–79	11.8	92	91

[a] Oregon Department of Fish and Wildlife (1982).
[b] McGie (1982a).
[c] McGie (1982b).
[d] Cramer and Boyce (1986).

Results and Discussion

Production of coho salmon from Oregon's coastal streams, under current habitat conditions, is about half the recruitment realized in the early 1900's (Table 1). This amounts to a reduction of about 500 000 fish. The method I used to calculate the change in abundance of coho salmon does not establish that habitat degradation caused the reduction. However, the extent of changes in coastal watersheds since the mid-1800's, particularly after the turn of the century, suggests that changes in fish habitat may explain a large part of the change in abundance.

The small coastal streams or smaller tributaries of larger streams, normally recognized as coho salmon habitat (Scott and Crossman 1973 and Moring and Lantz 1975), were generally not subjected to the effects of logging and road building until after 1910 when high-lead rigging allowed timber harvest in smaller watersheds and steeper slopes. Since timber harvest has had the greatest adverse effect on habitat in coastal streams (Bureau of Land Management 1985), estimates of recruitment based on catches prior to 1920 may be prior to major changes to habitat of coho salmon and reflect the production potential of largely pristine environments.

Estimates of predevelopment production of coho salmon in the Columbia River ranged from 903 000 to 1 780 000 fish based on a 67 and 50 % harvest rate, respectively (Northwest Power Planning Council 1986). My estimate of 1 385 000 coho is within the range estimated for the Columbia River. The similarity of production estimates from coastal rivers and the Columbia Basin is consistent with their similar amounts of coho habitat: 5 108 miles in the Columbia Basin (Lavier 1976) and 4 764 miles for Oregon's coastal basins (Oregon Department of Fish and Wildlife 1982).

The current estimate of production potential of chinook salmon is about 150 000 fish greater than the estimate of historical production. Chinook salmon prefer the main stem and larger tributaries of coastal streams (Scott and Crossman 1973; Nicholas and Hankin 1988), so their habitat was the first to be altered by logging, agriculture and settlement. Early streamside logging and the use of splash dams to move logs downstream was concentrated in the main stems of coastal rivers and, therefore, was particularly devastating to chinook salmon habitat. My estimate of historical abundance of chinook salmon may reflect production from habitats already severely degraded and of diminished productivity and, given the nature of this analysis, the small increase in chinook production may also be interpreted as no change in chinook stocks from the depressed conditions at the turn of the century. However, an increase in productivity of chinook salmon (Table 1) is consistent with the healthy condition of chinook salmon stocks (Salo and Rogers 1984) and may be evidence that their habitat is beginning to recover from earlier devastation. McGie (1981) observed that total spawning escapement of chinook salmon in Oregon's coastal streams has increased by about 3 % annually since 1950 (Fig. 1). A gradual, long-term increase in production would be consistent with a gradual recovery of physically damaged habitat combined with favorable ocean conditions and moderate harvest rates (Nicholas and Hankin 1988).

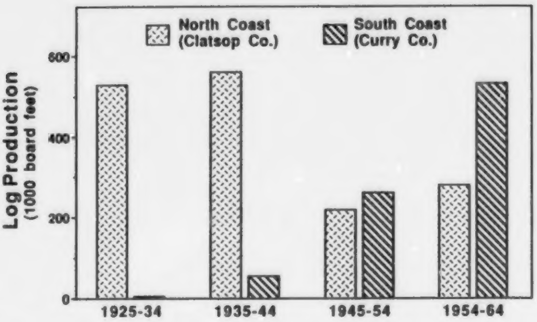

FIG. 1. Average escapement of chinook and coho salmon into Oregon's coastal streams, 1950–85 (from McGie 1985).

The increasing escapements of chinook salmon are primarily in north and midcoast streams, although not all of those streams are improving (Nicholas and Hankin 1988). Stocks of chinook salmon from the smaller streams on the south coast appear not to have increased (McGie 1985; Nicholas and Hankin 1988), possibly because of inadequate sampling (Oregon Coastal Zone Management Association 1985), because of overharvest of those stocks (Hankin et al. 1986), or because habitat degradation from logging occurred later on the south coast (Fig. 2) and the habitat in those streams has not recovered sufficiently to support increases in production of chinook salmon.

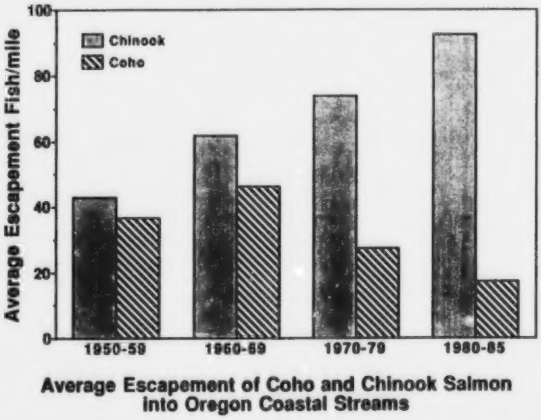

FIG. 2. Average log production during 10-yr intervals for Clatsop (North Coast) and Curry County (South Coast) (from Wall 1972).

Where juvenile coho and chinook salmon distributions overlap, coho salmon have a competitive advantage in the cooler sections of a stream and chinook salmon have an advantage in warmer sections (Stein et al. 1972). In the Sixes River, located on the southern Oregon coast, juvenile coho salmon vacated a logged tributary as water temperatures increased in the summer, whereas they reared through the summer in a cooler, unlogged tributary (Stein et al. 1972). Stream temperature increases when the forest canopy is removed and more solar radiation reaches the water surface (Moring and Lantz 1975). The removal of large organic debris can also eliminate cool-water refuges and result in further warming of coastal streams (Sedell and Swanson 1986). The physical condition of coastal streams prior to development, particularly the presence of beaver ponds, side channels, sloughs, and tangles of large woody debris (Sedell and Luchessa 1981) may have been productive habitat for coho salmon (Peterson and Reid 1984). The quality of these habitats for coho salmon was reduced when stream channels were cleaned to aid log transport and by the scouring effect of moving logs particularly when logs were moved in conjunction with splash dams. The net effect of logging — cleaned streams with few side channels and sloughs and higher water temperatures — may have contributed to a long-term shift from habitats favoring coho salmon to habitats favoring chinook salmon.

Although the analysis presented in this report is speculative, the results are generally consistent with other published information. The trends — decreasing coho abundance and increasing chinook abundance — and the magnitude of the changes in abundance, appear to be plausible estimates of the loss or gain in production since the turn of the century. Long-term changes in salmon abundance and the possible role of habitat should be taken into consideration in the implementation of habitat enhancement and protection programs. The time frame of most contemporary studies is too short to detect the effects of recovery of habitat (50–60 yr) or long-term shifts in abundance in response to habitat changes. The longest habitat study in Oregon, for example, has been 15 yr. The results of short-term studies need to be interpreted in the context of long-term changes. At a minimum, basic monitoring of fish and fish habitat are needed. Unfortunately, long-term inventories of stream habitat and salmon populations are still not a part of the management program in Oregon. Lacking adequate monitoring, biologists in the future will continue to rely on speculation to evaluate coast-wide changes in habitat and fishery status.

Acknowledgments

Jay Nicholas gave the author many constructive suggesstions during the preparation of the manuscript.

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The Use of Smolt Survival Estimates To Quantify the Effects of Habitat Changes On Salmonid Stocks in the Sacramento-San Joaquin Rivers, California

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Abstract

KJELSON, M. A., AND P. L. BRANDES. 1989. The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento–San Joaquin rivers, California, p. 100–115. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Mark–recapture studies of smolt survival in the Sacramento–San Joaquin Delta of California provides empirical data on the effects of water development on fall-run chinook salmon (*Oncorhynchus tshawytscha*). Recoveries of coded-wire tagged hatchery fish from the ocean troll fishery and estuarine trawling yielded two survival measures that were positively correlated (r=0.90). Smolt survival from both measures were highly correlated to river flow, temperature, and percent diversion. Survival of fish exposed to diversion was about 50 % less than those not exposed. Study designs to quantify the independent effects of temperature on survival and the survival of wild smolts are presented. Survival results are being used to evaluate estuarine flow standards governing state and federal water project operations and other salmon protective measures. Regressions of survival and flow applied to simulated historical flows at varied levels of water development indicated estuarine survival has decreased a minimum of 30 % in the past 70 yr. Spawner escapements in the Central Valley are positively correlated to flow during their spring smolt outmigration suggesting that flow alterations in upstream and estuarine habitats at that time influences adult stock production.

Résumé

KJELSON, M. A., AND P. L. BRANDES. 1989. The use of smolt survival estimates to quantify the effects of habitat changes on salmonid stocks in the Sacramento–San Joaquin rivers, California, p. 100–115. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Les études de marquage–recapture réalisées afin de déterminer le taux de survie des smolts dans le delta de Sacramento-San Joaquin, en Californie, fournissent des données empiriques sur les effets de la mise en valeur des ressources en eau sur la remontée des saumons quinnats (*Oncorhynchus tshawytscha*) à l'automne. La récupération des poissons d'élevage marqués au moyen de fil de fer codé dans la zone de pêche à la traîne en mer et dans la zone de pêche au chalut en estuaire a abouti à des taux de survie présentant une corrélation positive (r = 0,90). Une étroite corrélation a été établie entre, d'une part, les taux de survie des smolts dans les deux zones de pêche et, d'autre part, les taux de survie des smolts dans les zones de pêche et, d'autre part, le débit du cours d'eau, la température et le volume d'eau détourné. Le taux de survie des poissons exposés à des ouvrages de dérivation était inférieur à celui des poissons non exposés dans une proportion d'environ 50 %. On présente des plans d'étude destinés à quantifier les effets distincts de la température sur les taux de survie et les taux de survie des smoltssauvages. Les résultats servent à évaluer les normes relatives aux débits en estuaire auxquelles sont assujettis les projets de mise en valeur des eaux des États et du gouvernement fédéral et d'autres mesures de protection des saumons. Les coefficients de régression des taux de survie et du débit appliqués à des débits historiques simulés en fonction de divers degrés de mise en valeur des ressources en eau ont révélé que la survie en estuaire a diminué de 30 % au minimum au cours des 70 dernières années. Il existe une corrélation positive entre les échappées de géniteurs dans la vallée Central et le débit des eaux au cours de la dévalaison des smolts au printemps, ce qui laisse supposer que les modifications du débit dans les habitats d'amont et en estuaire pendant cette période influent sur la production des stocks d'adultes.

Introduction

Documenting effects of habitat alterations on salmonid stocks is difficult because each life stage is exposed to varied environmental conditions. Measurement biases and imprecision of estimates also contribute to this problem. Thus quantifying factors affecting adult population levels is often troublesome.

Mark/recapture experiments provide opportunity to measure effects of specific environmental conditions on survival. This eliminates the need to base evaluations on abundance changes which may reflect earlier environmental conditions or population levels (Stevens and Miller 1983). Evaluating factors influencing smolt survival afford a more direct means to assess habitat alteration/stock effects. In the absence of subsequent density dependent mortality (Junge 1970) these factors would directly affect the ocean recruitment and escapement.

Results of our studies on the survival of fall-run chinook salmon, *Oncorhynchus tshawytscha*, during their spring outmigration through the Sacramento–San Joaquin Estuary of California (Fig. 1) provides empirical data on the effects of water development activities that have changed the magnitude, distribution and timing of river flows. This work is part of the Interagency Ecological Study Program designed to document the needs of estuarine fishes, the impacts of water project diversions from the delta and the means to better protect fish and wildlife resources. Agencies within that program include the California Departments of Fish and Game, Water Resources, the State Water Resources Control Board, the U.S. Geological Survey, the U.S. Bureau of Reclamation, and the U.S. Fish and Wildlife Service.

Natural spawning chinook stocks have shown a general decline parallel with increased water development both upstream and in the estuary. Chinook salmon spawn in the major rivers of the Central Valley (Fig. 2). Total fall-run escapement has fluctuated greatly, ranging from 125 000 to 584 000 spawners between 1953 and 1986 (Dettman et al. 1987). Runs in the upper Sacramento River have declined to about 50 % of those in the 1950s. Conversely, long term escapement to the American and Feather rivers has been maintained or slightly increased (average about 40 000 in both systems) over the past thirty years. These tributaries are heavily supported by hatcheries and since the 1970's hatchery production from those rivers has been trucked downstream to the lower estuary for release, thus avoiding upstream and delta mortalities. Spawning levels in the San Joaquin tributaries have fluctuated greatly from about 2 000 to 84 000 since the 1950's.

A mark/recapture program based on coded-wire nose tagged (Jefferts et al. 1963) hatchery fish released under a variety of environmental conditions is being used to develop estimates of smolt survival in the Delta. These survivals are being correlated against river flows, percent diversion and river temperatures to investigate effects of environment on juvenile stocks. Tagged fish released above and below a major diversion point on the Sacramento River and in the diversion channels themselves provide direct measures of effects of physical changes in the migratory pathways. Correlations between escapement and river flow during smolt outmigration are being used to investigate effects of flow alterations on resulting adult stocks.

The major purpose of this paper is to (1) describe the survival methodology and evalute its validity, (2) share knowledge on the effects of estuarine water development on smolt survival, and (3) discuss management applications of resulting information.

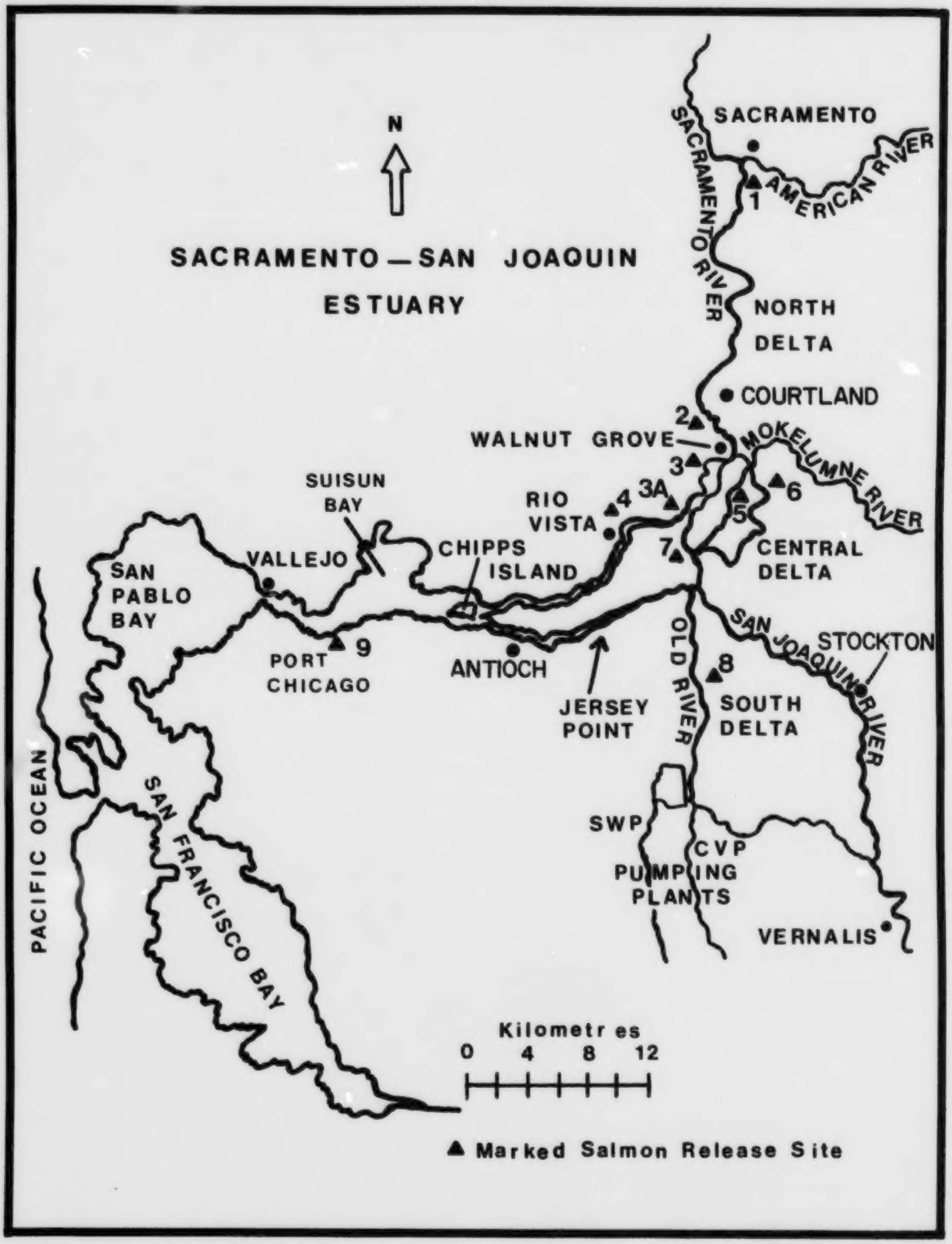
Study Area

The Sacramento–San Joaquin Estuary (Fig. 1) consists of the tidally influenced freshwater delta where the Sacramento and San Joaquin rivers join. It is comprised of 30 major man-made islands and about 1 200 km of channel, and a series of downstream embayments, Suisun, San Pablo, and San Francisco bays. Conomos (1979) and Kelley (1966) provide more detailed descriptions of the physical and biological characteristics of the estuary.

The historical annual flow passing through the estuary from its 163 000 km^2 drainage basin averaged about 1 100 $m^3 \bullet s^{-1}$ in 1900, but consumptive uses upstream and diversions from the Delta by 1960 had reduced that flow by about one-half (Chadwick 1977). The present pattern of seasonal river inflow to the Delta is modified by water storage in upstream reservoirs in the winter and spring. When natural runoff is less than reservoir storage capacity, delta inflow is controlled by project operations. This process often reduces inflows during the April–June outmigration period of salmon smolts.

The delta is the pivot point in the transfer of water from northern to southern California. The major out-of-basin diversions are made via the Federal Central Valley Project (CVP) and State Water Project (SWP) pumping plants in the southern delta (Fig. 1). The average percent of total delta inflow that has been diverted by the two projects during April through June since 1970 has ranged from about 16 % in wet years to 44 % in dry years. Typical May–June export rates of the two projects substantially exceed the delta inflow from the San Joaquin River, thus CVP/SWP export needs are not met by the San Joaquin basin runoff, and remaining project demands must be achieved by diversions of Sacramento River water.

Much of that flow is diverted from the Sacramento River at Walnut Grove into the central delta and southward toward the water project pumps via the Delta-Cross Channel (constructed by the CVP in 1951), Geor-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SACRAMENTO—SAN JOAQUIN ESTUARY
SACRAMENTO
AMERICAN RIVER
1
SACRAMENTO RIVER
NORTH DELTA
COURTLAND
2
WALNUT GROVE
MOKELUMNE RIVER
3
3A
4
RIO VISTA
5
6
7
CENTRAL DELTA
SUISUN BAY
VALLEJO
CHIPPS ISLAND
SAN PABLO BAY
9
PORT CHICAGO
ANTIOCH
JERSEY POINT
OLD RIVER
8
SAN JOAQUIN RIVER
STOCKTON
SOUTH DELTA
SWP
CVP
PUMPING PLANTS
VERNALIS
PACIFIC OCEAN
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Kilometres
0 4 8 12
▲ Marked Salmon Release Site

FIG. 1. The Sacramento–San Joaquin Estuary of California including marked salmon release sites.

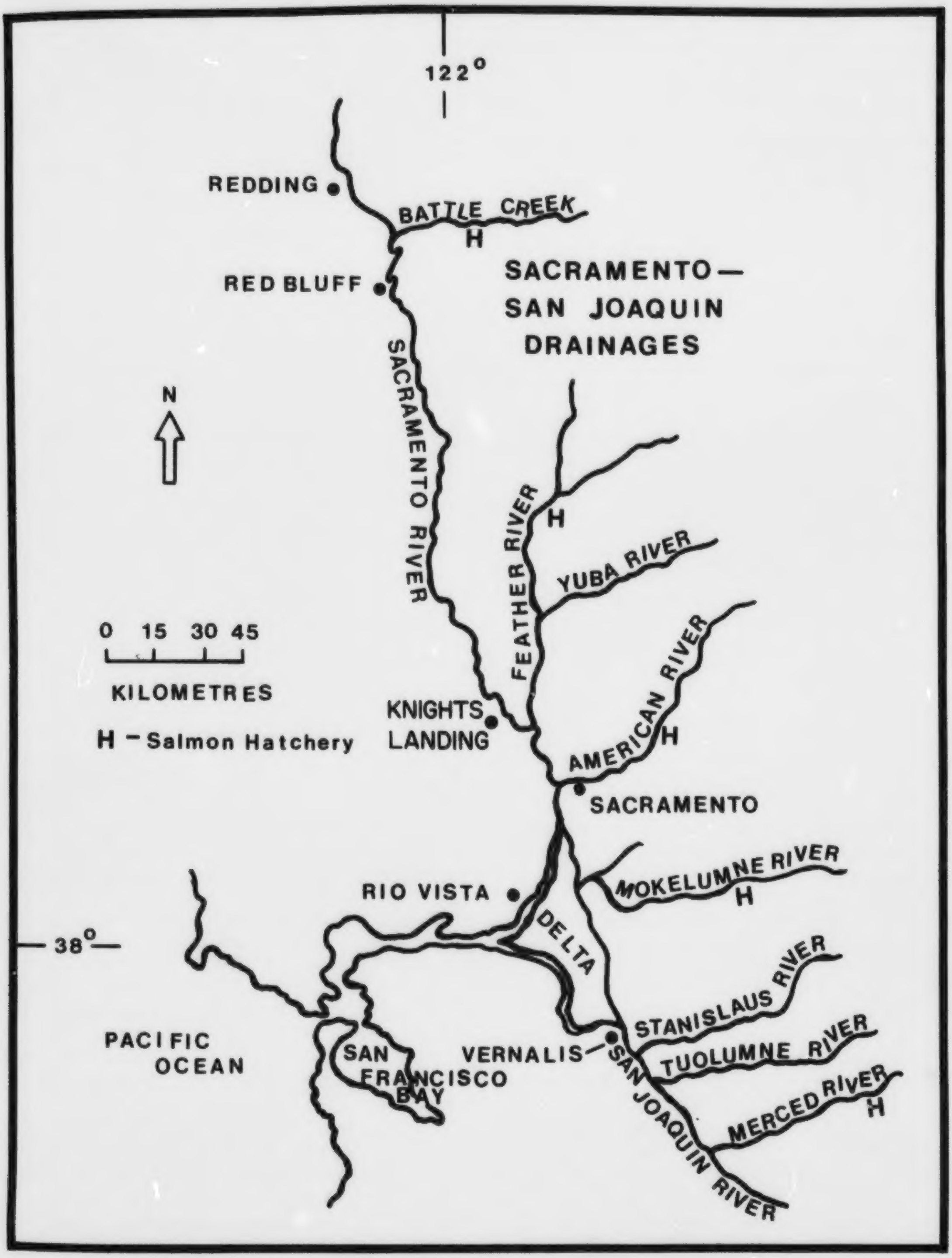
122°
REDDING
BATTLE CREEK
H
RED BLUFF
SACRAMENTO— SAN JOAQUIN DRAINAGES
N
SACRAMENTO RIVER
FEATHER RIVER
H
YUBA RIVER
AMERICAN RIVER
H
0 15 30 45
KILOMETRES
H – Salmon Hatchery
KNIGHTS LANDING
SACRAMENTO
MOKELUMNE RIVER
H
RIO VISTA
DELTA
38°
STANISLAUS RIVER
PACIFIC OCEAN
SAN FRANCISCO BAY
VERNALIS
TUOLUMNE RIVER
MERCED RIVER
H
SAN JOAQUIN RIVER

FIG. 2. Major chinook salmon spawning streams in the Sacramento–San Joaquin drainages of California.

giana Slough, and the natural channels of the central delta (Fig. 1 and 3). The percent taken from the Sacramento River at Walnut Grove during April through June has averaged 44 % (range 23–61 %) from 1978 to 1986.

Project export rates and central delta channel volume limitations causes additional Sacramento River water to be drawn upstream via the lower San Joaquin River past Antioch to the northern end of Old River (Fig. 1 and 3). Such net upstream (reverse) flows are typical in late May and June of dry years.

Methods

Physical Conditions

Flow and diversion rates in key delta channels were from published California Department of Water Resources (DWR) DAYFLOW records and formuli. Water temperature data were from the California Departments of Fish and Game (DFG) and Water Resources (DWR), U.S. Geological Survey and from our own measurements. DWR operational studies using hydrological models were used to simulate historic flows in the Delta at various levels of water project development by time period.

Smolt Survival

Marking

Fall-run hatchery chinook from the DFG Feather River Hatchery of a size similar to wild smolts (70–100 mm) (Kjelson et al. 1982) were marked with fin clips in 1969–71 and coded wire nose tags (CWT) and adipose clips from 1978 to 1987. During six study years, individual release groups were tagged with multiple codes to assess the precision of survival measures. From 50 000 to 250 000 smolts per release group were marked for release at selected sites in the delta and Suisun Bay.

Releases

Fall-run chinook salmon smolts in the Central Valley typically migrate to sea from April through June with the majority seen in the delta in May and early June (Kjelson 1982). Therefore, our marked smolt releases were made primarily in late May and early June. Fish released in the north delta at Sacramento or Courtland (Sites 1 and 2, Fig. 3) and at Rio Vista and Port Chicago (Sites 4 and 9, Fig. 1 and 3) were used to estimate survival in the delta. A single release was also made in May 1981 at Knights Landing (Fig. 2). Differences in recovery rate for those released above (Site 2) and below (Site 3) Walnut Grove were used to assess effects of the Cross channel–Georgiana Slough diversions. Tagged fish released in the central and southern delta (Sites 5, 6, 7, and 8, Fig. 3) represented those that had been diverted off the Sacramento River and were moving toward the pumping plants.

Similar procedures were used in the trucking, handling and releases of hatchery fish during each year although some unavoidable differences in truck temperatures (range 1–5°C) and travel time between hatchery and release site were observed (range 2–3 h). General condition of each release group at time of release was observed to assure no significant direct mortality had occurred. Tag codes were verified by sampling tagged fish at release sites.

We compared water temperatures between hatchery truck and release sites, and fish sizes for the treatment (Sacramento or Courtland sites) and control groups (Port Chicago Site 9, Fig. 1) to evaluate if release conditions might have biased survivals. Data were not available to test for specific differences in predation or food at release sites.

Recovery

Recoveries of tagged smolts were made within a few weeks after release by midwater trawling at Chipps Island (Fig. 1) and by sampling the ocean troll and sports fishery 2–5 yr later. Ten 20-min tows per day were made during day-light usually beginning the day the first fish of a tag group was recovered until no tagged fish of that group were recovered (this ranged from 5 to 36 days for each release group).

The midwater trawl had a 9.1 by 7.9 m mouth opening with a 3.2 mm mesh cod end, increasing to 102 mm mesh wings. It was spread by two surface and two midwater doors. The trawl fished approximately the upper one-half of the water column which is where over 90 % of the smolts were found during daylight (Wickwire and Stevens 1970). We assumed that survival indices from only daylight sampling represented survival for the total smolt migration (day and night). Engine speed was held constant during each tow to keep sample volume consistent. Flow meter reading varied by about ±10 % per tow (average coefficient of variation) indicating sample volumes were similar. Tows were typically made against the current except at slack tide. Water depth trawled ranged from about 8 to 15 m and channel width was about 1 200 m. Samples were taken across the entire channel with an equal number in south, middle, and north portions. This same trawl methodology was used to quantify the seasonal distribution and relative abundance of unmarked fall-run smolts migrating past Chipps Island for April, May, and June from 1978 to 1986.

Ocean tag recovery for 1969–71 was based on port sampling by the California Department of Fish and Game with tag recoveries expanded using reciprocals

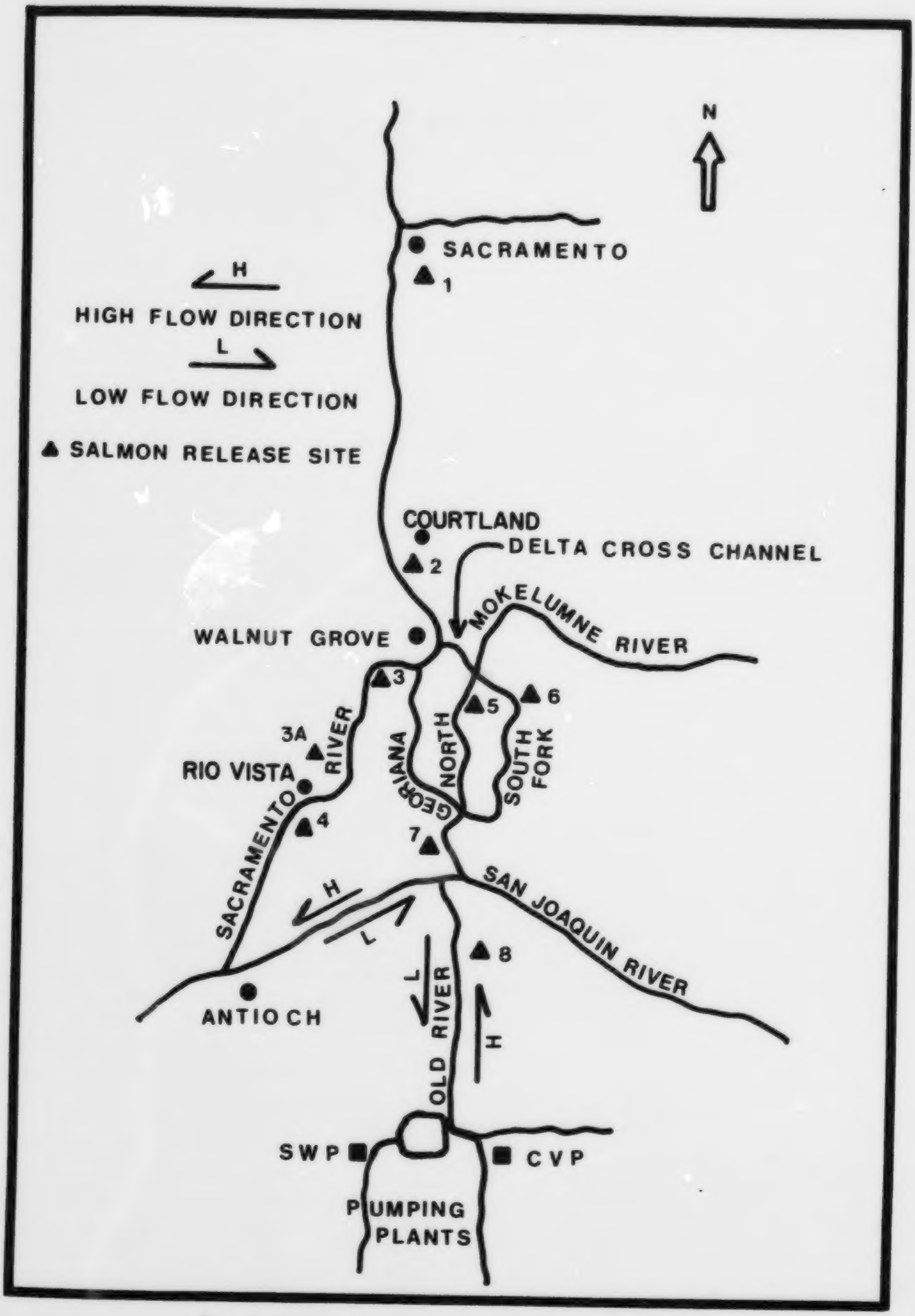
N
SACRAMENTO
1
H
HIGH FLOW DIRECTION
L
LOW FLOW DIRECTION
▲ SALMON RELEASE SITE
COURTLAND
DELTA CROSS CHANNEL
2
WALNUT GROVE
MOKELUMNE RIVER
3
5
6
3A
RIO VISTA
RIVER
GEORGIANA
NORTH
SOUTH FORK
SACRAMENTO
4
7
SAN JOAQUIN RIVER
H
L
8
L
OLD RIVER
H
ANTIOCH
SWP
CVP
PUMPING PLANTS

FIG. 3. Detail schematic of the major channels in the Sacramento–San Joaquin Delta including salmon release sites and flow direction in selected channels under high and low runoff conditions.

of port sampling fractions. Tag recovery data and procedures for other years are published by the Pacific Marine Fisheries Commission, 1400 S.W. 5th Ave., Portland, Oregon. We assumed tag groups were distributed equally throughout the fishery and exposed to the same harvest and sampling rates.

Survival Indices

Smolt survival through the Delta was measured using two mark–recovery methods. Our first survival measure, S_o was an estimate based on the tag recoveries of marked fish from the ocean fishery.

$$S_o = \frac{R_1/M_1}{R_2/M_2}, \text{ where:}$$

M_1 = number of tagged fish released in the Sacramento River in the north Delta (Sites 1 or 2)
R_1 = ocean recoveries of M_1
M_2 = number of tagged fish released in western delta or Suisun Bay (Sites 4 or 9)
R_2 = ocean recoveries of M_2

These calculations assume all fish had equal survival probability west of the downstream release points (Sites 4 and 9) and that differences in the tag recovery rates reflect mortality of the upstream groups as they migrated through the delta.

An arc–sine transformation was made to S_o to remove potential bias due to the constraints of proportions (Zar 1984).

Our second delta survival measure, S_T, is an index of the number of tagged fish passing Chipps Island based on trawl recoveries and corrected for sample effort in time and space.

S_T = R/MT (0.0078) where,
R = number of tagged fish recovered by trawl for each release group
M = number released for each release group
T = fraction of time sampled (10–14%) when the fish were passing Chipps Island.

The constant 0.0078 = trawl width (9.1 m) divided by mean channel width (1167 m). Channel width is essentially constant at all tides and flows. Variation in trawl width is unknown but we assumed it random and part of variation in S_T. S_T was used to index survival from varied delta release sites to Chipps Island. S_o and S_T were correlated from the same release groups from 1978 to 1984.

Spawner Escapement

Central Valley spawner escapement levels were based on counts of fish entering hatcheries, migrating past dams, carcasses and live fish on spawning grounds, and aerial redd counts (1953–69: Taylor 1973; 1964–81: Reavis 1983; 1970–84: Pacific Fisheries Management Council 1985). Central Valley chinook salmon return to spawn at ages ranging from primarily 2 to 5 yr. Returns of known age (coded wire tagged) spawners indicate that most are 3-yr-old (Reisenbichler 1986). Hence, we used a $2^1/_2$-yr lag between the time of smolt migration and escapement in correlating flow and escapement.

Results

Survival Indices

Detailed release, recovery, tag code and survival information, as supporting background data for each tagged smolt release group, is available from the authors.

The variability characterizing our two survival measures was based on the available data from replicate tag groups (Table 1). It appears relatively small compared to the variation in the annual survival estimates. Our limited replicates made it difficult to test for differences in annual survivals.

Survival estimate, S_o, was highly correlated with survival index, S_T, with an r=0.90 for survivals between the north delta and Suisun Bay for 1978 to 1984 data. This indicates that two, essentially independent methods yield survivals that are closely related providing support for the validity of both measures.

Bias in our survival estimates associated with differences in water temperature in the truck and release sites appeared minimal (Table 2). In all years the "thermal shock" experienced by the tagged fish was relatively high (4.5–11.1°C) and in 1981 the fish were released in obviously adverse temperatures of 23.9 and 24.5°C that were near lethal (Brett 1952; Orsi 1971). Nevertheless, in the 6 yr evaluated, the temperature differentials were small between the upstream and downstream release sites (0.5 to 5°C, Table 2) suggesting little bias.

Biases associated with differences in tagged fish size at upsteam and downstream release sites also appeared minimal (Table 3). Size differences for 7 of the 11 yr evaluated were very small (0–4 mm) and somewhat higher in other years (8–13 mm). We concluded that such bias did not invalidate the relations between survival and flow, diversion and temperature described below.

Survival: Habitat Relationships

Effects of Flow

Based on ocean tag recoveries, the survival of smolts through the delta from Sacramento to Suisun Bay was

TABLE 1. Summary of the recovery rates of marked fish from both ocean and trawl recoveries and the associated variability around estimates of survival, S_o and, S_T when multiple tag codes were used.

Year	Release site	CWT Code	Recovery rate	Mean recovery rate	Ocean Recovery Estimate Survival estimate (S_o)	Minimum and maximum estimate of survival	Survival index (S_T)
1980	Sacramento	6-62-8	0.0107	0.0100			0.33
	Sacramento	6-62-11	0.0092				0.35
	Port Chicago	6-62-09	0.0232	0.0243			
	Port Chicago	6-62-12	0.0253				
					0.41	0.36 to 0.46	
1981	Sacramento	6-62-14	0.0003	0.0003			0.02
	Sacramento	6-62-17	0.0003				
	Port Chicago	6-62-15	0.0279				
					0.01	0.0115 to 0.0122	
1982	Sacramento (CNFH)[a]	6-62-18	0.0120	0.0135			1.53
	Sacramento (FRH)[a]	6-62-20	0.0150				1.48
	Port Chicago (CNFH)	6-62-19	0.0091		1.49	1.33 to 1.66	
1984	Courtland	6-62-27	0.0053				NA[b]
	Port Chicago	6-62-31	0.0040	0.0060			
	Port Chicago	6-62-37	0.0080				
					0.89	0.66 to 1.33	
1985	Courtland	6-62-38					0.39
	Courtlant	6-62-39			NA		0.13
	Courtland	6-62-40					0.26
	Courtland	6-62-41					0.41
1987	Courtland (gates closed)	6-62-53			NA		0.60
	Courtland (gates closed)	6-62-54					0.72
	Courtland (gates opened)	6-62-56			NA		0.39
	Courtland (gates opened)	6-62-57					0.42

[a] Fish produced from Coleman National Fish Hatchery and Feather River Hatchery.

[b] NA = Not Available.

TABLE 2. Temperatures in hatchery truck and receiving waters (in degrees centigrade) experienced by tagged salmon used in survival estimates released above and below diversions and based on ocean tag recoveries.

Year	Release site	Truck temp.	Receiving water temp.	Temperature difference
1969	Sacramento	—	18.6[a]	—
	Rio Vista	—	20.4	—
1970	Sacramento	—	21.4[a]	—
	Rio Vista	—	19.4	—
1971	Sacramento	—	16.4[a]	—
	Rio Vista	—	15.6	—
1978	Sacramento	13.9	22.6	8.7
	Port Chicago	13.9	19.9	6.0
1979	Sacramento	12.2	20.0	
	Port Chicago	—	—	7.8
1980	Sacramento	11.1	16.7	5.6
	Port Chicago	13.9	21.1	7.2
1981	Knights Landing	—	17.8	—
	Port Chicago	12.8	23.9	11.1
1981	Sacramento	13.9	24.5	10.6
	Port Chicago	12.8	23.9	11.1
1982	Sacramento	13.4	20.0	6.6
	Port Chicago	13.9	19.5	5.6
1983	Courtland	11.1	15.6	4.5
	Port Chicago	10.0	19.5	9.5
1984	Courtland	13.9	18.9	5.0
	Port Chicago	15.0	22.3	7.3

[a] Temperatures taken 10 km below Sacramento.

TABLE 3. Mean length and size differences of tagged salmon released above and below diversions and based on ocean tag recoveries.

Year	Release Site	Mean length (mm)	Difference in mean length (mm)
1969	Sacramento	89.7	1.0
	Rio Vista	88.7	
1970	Sacramento	86.5	
	Rio Vista	86.5	0.0
1971	Sacramento	86.0	8.5
	Rio Vista	77.5	
1978	Sacramento	90.9	1.8
	Port Chicago	89.1	
1979	Sacramento	74.5	−8.7
	Port Chicago	83.2	
1980	Sacramento	96.9	9.1
	Port Chicago	87.8	
1981[a]	Knights Landing	77.0	−13.1
	Port Chicago	90.1	
1981	Sacramento	89.7	−0.4
	Port Chicago	90.1	
1982	Sacramento	76	4.0
	Port Chicago	72	
1983	Courtland	79	−3.0
	Port Chicago	82	
1984	Courtland	82	0.0
	Port Chicago	82	

[a] Released in May.

highly correlated to mean daily Sacramento River flow at Rio Vista ($r=+0.85$, Fig. 4). Survival, S_o, increased rapidly with an increase in flow from about 200 to 650 $m^3 \bullet s.^{-1}$ where survival appears maximum. Smolt survival remains at about 100% at Rio Vista flows over 650 $m^3 \bullet s.^{-1}$. Survival values over the theoretical maximum of 100% for 1982 and 1983 may reflect sampling imprecision or some unknown bias.

The values for 1983 and 1984 probably are biased high relative to other years since they are for fish released about 42 km downstream of Sacramento (at the "Courtland" site) and thus traveled a shorter distance than smolts released in earlier years at Sacramento. Survival indices in 1984 probably are more biased than in 1983, since flows were much lower in 1984.

Our second measure of smolt survival through the delta, that based on tag recoveries from trawling at Chipps Island, also was well correlated with flow ($r=0.83$, 1978 to 1987).

Mechanisms for the Flow: Survival Relationship

Several factors could cause the strong correlations observed between survival and flow. These include

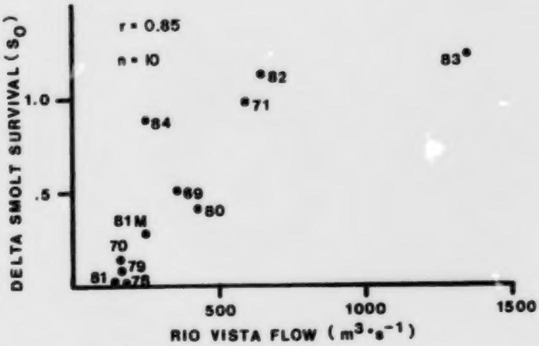

FIG. 4. Relationship between marked chinook smolt survival, (S_o), through the Sacramento–San Joaquin Delta and flow at Rio Vista, California during May or June for 1969–1971, and 1978–1984. May and June releases in 1981 labeled 81M and 81, respectively. 1983 survival data were not included in calculation of the correlation coefficient since survival does not appear to increase over 650 cms. An arc–sine transformation was made to S_o to remove potential bias due to the constraints of proportions (Zar 1984). While r value shown is based on untransformed S_o values, arc–sine transformed S_o yielded an $r=0.87$.

diversion, temperature, turbidity, and toxicity. High flows would dilute pollutants while the increase turbidity associated with greater flows would lessen predation. Both could potentially increase smolt survival but we could not evaluate these hypotheses due to lack of data.

Our emphasis has been to evaluate the independent effects of diversion and temperature on survival since flow, diversion and temperature are all strongly correlated with each other (absolute r = 0.74–0.79) making it difficult to use correlation techniques to separate the relative roles of these three factors on survival. Quantifying the independent effects of each factor requires experimental approaches and will help to identify the most effective restoration measures.

Effects of Diversion — Smolt survival, S_o, in the delta was negatively correlated (r=-0.63) with the percentage of water diverted from the Sacramento River at Walnut Grove via the cross channel and Georgiana Slough (Fig. 5 and 3).

We also found that in all four years (1984, 1985, 1986, and 1987), under high diversion rates (>60%) with the delta cross channel gates open, the survival of smolts (S_T) released above the diversion was about 50% less than for those released below the diversion (Table 4). When the cross channel gates were closed, preventing diversion through that channel, there was no difference in survival of these two groups during the high flow year of 1983, and about a 25% difference in the very low flow year of 1987 presumably due to the effect of diversion via Georgiana Slough.

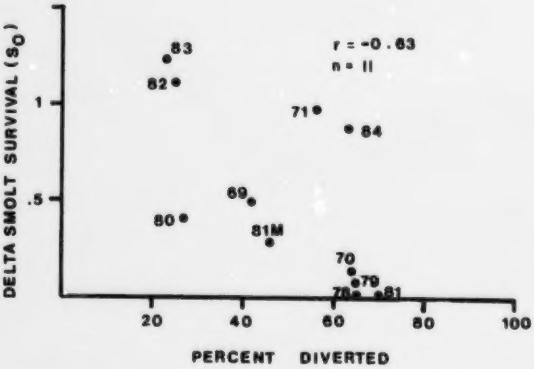

FIG. 5. Relationships between marked chinook smolt survival, S_o, through the Sacramento–San Joaquin Delta and thepercent diverted from the Sacramento River at Walnut Grove, California during May or June 1969–1971 and 1978–1984. An arc-sine transformation was made to S_o to remove potential bias due to the constraints of proportions (Zar 1984). While the r value shown is based on untransformed S_o values, arc-sine transformed S_o yielded an r=-0.63.

TABLE 4. Survival indices of coded wire tagged (CWT) chinook smolts released at several locations in the Sacramento–San Joaquin Delta from 1983 to 1987 and recovered by trawl at Chipps Island.

Release Site	1983	1984	1985	1986	1987
Above Diversion[a] gates opened	—	0.61	0.34	0.35	0.40
Above Diversion gates closed	1.06	—	—	—	0.67
Below Diversion[b] gates opened	—	1.05	0.77	0.68	0.88
Below Diversion gates closed	1.33[c]	—	—	—	0.85[b]
North Fork Mokelumne R.[d]	NR	0.51	0.28	0.36	NR
South Fork Mokelumne R.[d]	NR	0.86	0.23	0.26	NR
Lower Mokelumne R.[e]	1.13	NR	NR	NR	NR
Lower Old River R.[f]	0.33	0.16	0.21	0.23	NR

[a] Release Site 2 on Fig. 3.
[b] Release Site 3 on Fig. 3.
[c] Release Site 3A on Fig. 3.
[d] Release Sites 5 and 6 on Fig. 3.
[e] Release Site 7 on Fig. 3.
[f] Release Site 8 on Fig. 3.
NR = No Release.

TABLE 5. Diversion and flow conditions in the north, central and southern Sacramento–San Joaquin Delta from the period that marked fish released at Courtland (Site 2 on Fig. 3) were travelling to Chipps Island (1983 to 1987).

	1983	1984	1985	1986	1987-O[f]	1987-C[f]
Percent Diverted[a]	23	62	65	64	69	29
Sacramento R. Flow[b]	1352	256	203	219	149	270
San Joaquin Flow[c]	1013	19	17	135	−23[h]	-58[h]
Temperature[d] above Diversion	15.6	18.9	17.8	22.8	19.2	19.2
Temperature[d] below Diversion	16.1	18.9	18.9	23.4	17.8	19.5
Temperature[e], Mokelumne R.	16.7	21.1	17.8	21.1	NR[g]	NR
Temperature[d], Lower Old R.	17.2	23.9	20.0	23.4	NR	NR

[a] from Sacramento River at Walnut Grove.

[b] at Rio Vista ($m^3 \bullet s^{-1}$).

[c] at Jersey Point ($m^3 \bullet s^{-1}$).

[d] °C at release site.

[e] mean at North Fork and South Fork Mokelumne River.

[f] O = Cross channel gates opened; C = Cross channel gates closed, reflects conditions during 3 day gate closure.

[g] NR = No Release.

[h] Upstream flows.

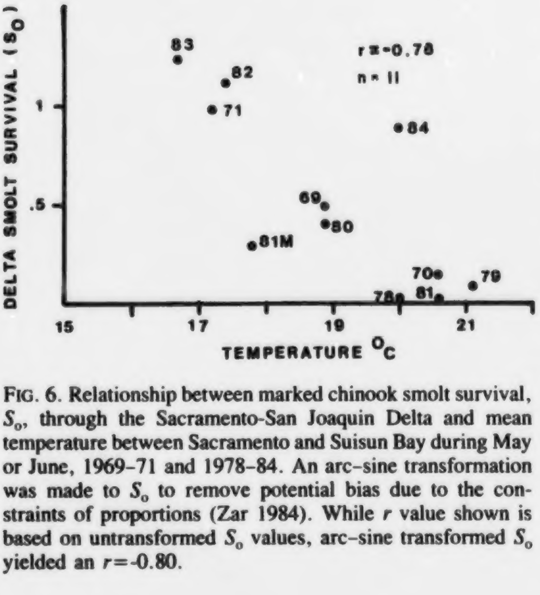

FIG. 6. Relationship between marked chinook smolt survival, S_0, through the Sacramento-San Joaquin Delta and mean temperature between Sacramento and Suisun Bay during May or June, 1969–71 and 1978–84. An arc–sine transformation was made to S_0 to remove potential bias due to the constraints of proportions (Zar 1984). While r value shown is based on untransformed S_0 values, arc–sine transformed S_0 yielded an r=-0.80.

Release temperatures at the sites above and below the diversion point in a given year were nearly identical indicating that the survival differences were due to the diversion process and not to temperature differences in the Sacramento River (Table 5). The 1987 data indicate that closing the cross channel even during low flow years can yield a major increase in delta smolt survival. These results indicate that diversions account for a part of the flow: survival relationship.

Tagged smolts released in the central delta had survivals slightly lower than those released above the point of diversion at Site 2 during 1985 and 1986 while data from 1984 indicated survivals were similar (Table 4). The group of tagged smolts released in lower Old River (Site 8, Fig. 3) had the lowest survival indices of all release groups for all years (Table 4).

Effect of Temperature — We found that smolt survival in the delta also was correlated to mean water temperature between Sacramento and Suisun Bay (r=-0.78, Fig. 6). The highest temperatures experienced by smolts are in late May and June. We have not been able to quantify the effects of temperature alone on survival but have plans to attempt this as discussed later.

Estimated Historical Survival — To evaluate how water development has affected smolt survival over the past 70 plus years we regressed smolt survival estimates (S_0) on Sacramento River flow at Sacramento. From this regression, estimates of the average smolt migration pattern by month (Table 6), and estimates of historic monthly flows at Sacramento, we calculated average survivals under four water development scenarios. These are: no development, 1920 level, 1940 level and 1990 level.

The results indicate that reduced inflow to the delta caused by water development in the Sacramento Valley

TABLE 6. Distribution in (percent) of total midwater trawl catch (April through June) of unmarked fall run smolts by month at Chipps Island in 1978—1986.

Year	April	May	June
	Percent of Catch		
1978	27	40	33
1979	19	52	29
1980	14	34	52
1981	34	50	16
1982	18	49	33
1983	19	49	32
1984	11	66	23
1985	26	63	11
1986	37	55	8
mean (1978-86)	22	51	17

has reduced smolt survival (Table 7). The greatest difference, as expected, are in the dry and critical years. The estimated maximum decrease in survival associated with the 1990 level of water development is about 40% (no development versus 1990). We estimated that survival decreased about 30% between 1940 and 1990. These are minimal estimates of decreases in survival as they do not account for the greater survival per unit flow that would have occurred before the delta cross channel began diverting a significant portion of the Sacramento River flow in the 1950's.

Discussion

Survival Methodology

Feasibility and Validity

The preceeding description of studies in the Sacramento—San Joaquin delta of California indicate that given appropriate funding and personnel, juvenile salmonid survival estimates are attainable. Costs associated with this approach, however, are high relative to abundance surveys when fish production, tagging and tag retrieval and decoding are considered. Each step in the mark/recapture process involved complex logistics. Extensive coordination between hatchery personnel, biologists, sampling crews and boat operators was essential to meet experimental design criteria. Recovering tagged smolts by trawling has the advantage of obtaining results without having to wait for the fish to enter the ocean fishery. It also provides an opportunity to estimate survival using two methods which forms a basis for evaluating the validity of our survival estimates.

The use of tagged hatchery smolts to investigate factors affecting wild fish seems appropriate. Ideally, we would have tagged wild smolts but found great difficulty in collecting sufficient numbers that were in good health. As noted earlier, both of our approaches to estimate survival provided essentially identical results lending validity to our conclusions relative to the factors affecting survival.

In an attempt to address this concern, we have plans

TABLE 7. Average estimated Delta survival indices of fall-run chinook smolt by water year type at different levels of development: unimpaired (no development), and at 1920, 1940, and 1990 levels of development.[a]

Water year types	(Sample size)	Unimpaired no development	1920 level of development	1940 level of development	1990 level of development
Wet	(19)	0.97	0.92	0.91	0.83
Above normal	(10)	0.91	0.85	0.83	0.61
Below normal	(10)	0.84	0.69	0.66	0.41
Dry	(10)	0.76	0.57	0.55	0.33
Critical	(8)	0.33	0.17	0.21	0.12
Mean		0.76	0.64	0.63	0.46

[a] Annual survivals were estimated by weighting monthly survival indices by the average percent from 1978 to 1986 of total outmigrants going to sea (Table 6). Monthly survival indices were estimated from monthly flows using the linear relationship between salmon survival and flow at Sacramento where $y = 0.00005X - 0.465$ when y = survival and x = mean monthly Sacramento River flow. Data from 1969–71 and 1978–81 was used to derive the equation. Monthly flows for the four different levels of development was obtained from California Department of Water Resources planning simulation model studies (personal communication, 1416 Ninth Street, Sacramento, CA).

TABLE 8. Mean catch of chinook salmon smolts per 20 min tow with the midwater trawl at Chipps Island during April, May and June from 1978 to 1986.

Year	April	May	June	Flow (mean April, May, June at Rio Vista)	Annual mean[a]	Mean temp.[b]	Percent Diverted[c]
1978	23.1	34.0	27.6	541	28	63	45
1979	14.9	41.6	23.2	257	25	63	55
1980	5.6	14.0	21.1	394	17	62	38
1981	17.3	25.3	8.3	249	15	67	55
1982	18.9	51.7	34.6	1490	38	60	27
1983	24.8	65.0	42.8	1566	48	57	23
1984	3.2	20.0	7.0	302	10	64	50
1985	10.3	24.7	4.1	203	20	66	61
1986	22.5	32.9	4.7	356	24	65	44

[a] Total catch divided by the total number of tows for April through June.

[b] Degrees Fahrenheit, Sacramento River at Freeport (mean April through June).

[c] Percent of the Sacrament River diverted at Walnut Grove (mean April through June).

to measure survival of unmarked, wild smolts in the delta. The general approach would sample wild smolts by midwater trawl at both Sacramento (Site 1, Fig. 3) and at Chipps Island throughout the April–June migration period and to use the catch per unit effort ratios of the Sacramento site divided by the Chipps Island site to provide a survival index. A lag factor of about one week applied to the Chipps Island data would be used to correct for migration time. Results could be very useful in evaluating past survival: habitat relationships and the method would yield numerous measures of survival as environmental conditions change between April and June.

Our evaluations suggest that the survival measures are not influenced unduly by extraneous procedural factors. Potential bias associated with "temperature shock" at release sites and differences in fish size appeared only minimal. Hence we believe our survivals and correlations between survival and flow, temperature, and diversion are sound.

Habitat Alteration Effects

Survival: Habitat Relationships

Relatively high coefficients of correlation (absolute $r=0.52$–0.85) between smolt survival and flow, temperature and diversion for both S_0 and S_T provides evidence that one or a combination of two or more of these factors working together has a major influence on smolt survival in the Sacramento River delta. Even after arcsine transformation, highest survivals were observed when flows were high and temperatures and diversions were low. The relationships between wild smolt abundance at Chipps Island and flow ($r=0.89$). Temperature ($r=-0.83$) and diversion ($r=-0.77$) for the years 1978 to 1986 are added support for the above conclusions ($P<0.05$ in all cases) (Table 8). The three sets of correlations between S_o, S_T and smolt abundance and flow, temperature and diverison were consistent and are in the directions one would expect, lending validity to our conclusions.

Diversion — Schaffter (1980) found densities of salmon in the Sacramento River above the diversion channels at Walnut Grove were similar to those in the delta cross channel suggesting that fish were diverted in proportion to the flow split at that location. Smolts diverted into the central delta must travel a longer route and are exposed to increased predation. The higher temperatures of the central delta, more agricultural diversions and more complex channel configurations, also may reduce their ability to survive. In addition, upon reaching the mouth of the Mokelumne on the lower San Joaquin River they are often exposed to upstream (reverse) flows moving to the south via Old River toward the project pumping plants and sometimes to reverse flow in the San Joaquin River itself (Table 5, Fig. 3).

Tagged smolts released in the southern delta (Site 8) had the lowest survival of all release groups for all years which probably reflects more harsh conditions in the southern delta. Higher water temperatures and reverse flows (Table 5), predation near the south Delta Project fish screens (Hall 1980; R. Kano, DFG, pers. comm., same address as Kjelson/Brandes) and smolt mortality associated with the fish screen salvage process (Menchen 1980; P. Raquel, DFG, pers. comm., same address as Kjelson/Brandes) all may contribute to these high mortalities.

Temperature — High temperatures in the delta that approach lethal levels in June of low runoff years also play some yet unquantified role in smolt mortalities. Chinook salmon are stressed as temperatures rise and temperatures over 18°C are usually considered undesirable for juvenile chinook (Brett et al. 1982; Banks et al. 1971). Temperatures acutely lethal to chinook salmon smolts are about 24°C (Brett et al. 1982; Orsi 1971). Energy needs also increase as temperatures rise (Brett et al. 1982) thus food may be more limiting as temperatures increase. Chinook smolts consume both insects and zooplankton during their estuarine migration (Kjelson et al. 1982). We do not have sufficient data to evaluate if food densities of either type are limiting to smolts during their week long migration through the delta but it is possible.

Since many of our CWT smolt releases were made from mid-May to early June when temperatures were often high, it is possible that the flow: survival relationship in Fig. 4 does not apply to April and early May when temperatures are lower. If high temperatures are a major cause of the lower survival at low flows then the smolt survival for April and early May would be expected to be somewhat higher at low flows than our results indicate.

We plan to initiate cooperative efforts with the State (SWP) and Federal (CVP) water project operators so we can release tagged smolts in April and June under identical flow and diverison conditions. This will be possible in drier years when the river flows in April and June are under the control of project operations through reservoir releases. The temperature differences between April and June will thus enable us to quantify the changes in survival attributed to temperature alone.

Spawner: Flow Relationships — Relationships between salmon spawner escapements and flow during the smolt outmigration period reflect the importance of flow on smolt survival. Positive correlations between longterm escapements of Central Valley fall-run chinook and flow during the smolt migration period were observed (Table 9, Fig. 7 and 8).

The correlation between escapement and flow in the upper Sacramento appears to have declined in recent years (1968–81) due to recent water development changes (see Reisenbichler, 1989). The relationships for Feather and American river stocks were strengthened when the portion of the escapement attributed to

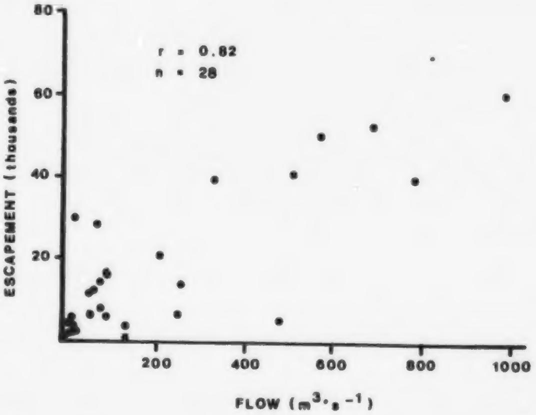

FIG. 7. Spring flows at Vernalis, California (mean April through June) experienced by the smolt outmigrants from 1956 to 1984 and the resulting San Joaquin fall-run chinook salmon escapement in 1958–86 (2½ yr lag).

TABLE 9. Correlations between fall-run chinook spawner escapement and flow during smolt outmigration for various stocks in California.

Stock	Flow period	Years	*r*	Reference
Upper Sacramento River	May[b]	1952–81	0.59[a]	Dettman et al. (1987)
	May[b]	1952–67	0.59[a]	"
	May[b]	1968–81	0.15	"
Feather River	June[b]	1952–81	0.31[a]	Dettman et al. (1987)
Feather River[e]	June[c]	1964–81	0.48[a]	Dettman & Kelley (1987)
American River	June[b]	1952–81	0.03	Dettman et al. (1987)
American River[e]	June[c]	1967–81	0.49	Dettman & Kelley (1987)
San Joaquin Tributaries	April–June[d]	1956–84	0.82[a]	Figure 7
Total Central Valley	May[b]	1960–86	0.47[a]	Figure 8

[a] Correlation significant at $P<0.05$ or less.

[b] Flow measured at Chipps Island.

[c] Flow measured in the northern delta.

[d] Flow measured at Vernalis.

[e] Estimates of hatchery contribution released below Walnut Grove diversion based on coded wire tag recoveries were omitted from escapement.

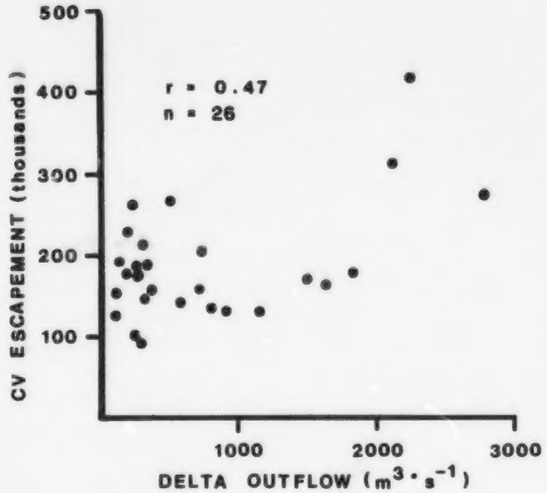

FIG. 8. The relationship between Central Valley fall-run chinook salmon escapement in 1960–86 versus May Delta outflow experienced 2^1/2 yr earlier (1958–84) by smolt outmigrants.

hatchery fish that was not exposed to the delta diversion at Walnut Grove was omitted.

The best long term correlation observed was for the San Joaquin tributaries (Fig. 7), a system that is highly developed with little hatchery contribution and where large escapements are only seen after high runoff during the smolt migration 2^1/2 yr earlier. Work by the California Department of Fish and Game (Bill Loudermilk, Region 4, 1234 E. Shaw Avenue, Fresno, CA, pers. comm.) indicates that salmon escapement in the Tuolumne River (Fig. 2) per unit of spring river flow during smolt migration has decreased over time (1939–86). This suggests that the increased habitat alterations both upstream and in the estuary over that period has decreased adult stocks. The correlation for total Central Valley stocks is surprisingly good considering the multitude of inland factors influencing adult production. In addition, the relationships are further impacted by imprecise and biased escapement estimates and variation in ocean survivals.

Management Applications

Our smolt survival results have been the basis for formal testimony presented to the State Water Resources Control Board during ongoing hearings to evaluate and revise present water quality and flow standards designed to protect salmon and other beneficial uses in the estuary.

The results also are being used to evaluate potential operational and structural protective measures such as flow pulses, decreased diversion rates, temperature controls, fish screens and channel barriers. Smolt survival information has encouraged a diverse cooperative effort between biologists, engineers, water managers and regulators to evaluate the cost and benefits to both fishery and water interests of varied management options. The planned studies described earlier to evaluate the relative importance of temperature and diversion are a result of this cooperation. This also has led to new evaluations of salmon restoration opportunities in upstream areas in the Sacramento and San Joaquin Valleys, in an attempt to gain a comprehensive Central Valley salmon restoration plan.

Use of survival data has also been made in varied modeling efforts on Central Valley salmon designed to evaluate the long-term stock benefits of increased flows, lesser diversion levels and other restoration measures in the delta and upstream drainages.

Results of our estimations of historical survivals reflecting alterations in flow can potentially be used to set goals for stock restoration although major philosophical/management questions arise relative to the level of restoration desired. Potential salmon management goals in the delta include specified smolt survival levels to be met by various protective measures.

Acknowledgments

We thank the many seasonal aids, boat operators, and hatchery personnel for their assistance. General encouragement and advice in analysis and data interpretation by P. Chadwick, D. Dettman, Dr. R. Brown, D. Kelley, D. Kohlhorst, Dr. R. Reisenbichler, and K. Urquhart was most helpful. We are indebted to D. Stevens for his critical review of the manuscript and continued advice. Support by S. Herrgesell and A. Eden in typing the manuscript and by K. Odenweller who drew the figures is greatly appreciated. This research was supported by the Interagency Ecological Study Program for the Sacramento–San Joaquin Estuary.

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Chinook Salmon (*Oncorhynchus tshawytscha*) and Estuarine Habitat: a Transfer Experiment Can Help Evaluate Estuary Dependency

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Abstract

LEVINGS, C. D., C. D. MCALLISTER, J. S. MACDONALD, T. J. BROWN, M. S. KOTYK, AND B. A. KASK. 1989. Chinook salmon (*Oncorhynchus tshawytscha*) and estuarine habitat: a transfer experiment can help evaluate estuary dependency, p. 116–122. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

In 1983, 1984 and 1985 marked juvenile chinook were released into riverine, estuarine, transition, and marine habitats in the vicinity of Campbell River, B.C. The experiment was designed to provide data on survival, to catch and escapement, of chinook deprived of estuarine habitat. Results up to mid March 1988 from returns to the commercial and sport fishery ($n = 365$) and returns to the river ($n = 273$) are evaluated. Differences in returns from the four release groups were statistically significant ($P<0.05$) in 1983 and 1984, when most recoveries were from river and estuary releases. For 1985, recoveries from the four release areas were not significantly different ($P>0.05$). Results are preliminary as adult returns are expected until 1991.

Résumé

LEVINGS, C. D., C. D. MCALLISTER, J. S. MACDONALD, T. J. BROWN, M. S. KOTYK, AND B. A. KASK. 1989. Chinook salmon (*Oncorhynchus tshawytscha*) and estuarine habitat: a transfer experiment can help evaluate estuary dependency, p. 116–122. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

En 1983, 1984 et 1985, des quinnats juvéniles marqués ont été libérés dans des habitats situés dans les cours d'eau, en mer et en estuaire ainsi que dans des habitats de transition, dans les environs de la rivière Campbell, en Colombie-Britannique. L'étude visait à recueillir des données sur les quinnats qui échappent aux captures et les échappées de quinnats n'ayant pas accès à des habitats en estuaire. Les estimations faites jusqu'à la mi-mars 1988, d'après les retours dans les zones de pêche commerciale et sportive ($n = 365$) et dans le cours d'eau ($n = 273$) sont évalués. Les différences observées en ce qui concerne les retours des quatre groupes libérés étaient statistiquement significatives ($P < 0{,}05$) en 1983 et 1984, au moment où la majorité des poissons recueillis appartenaient aux groupes libérés dans le cours d'eau et en estuaire. En 1985, aucune différence significative n'a été repérée relativement aux récupérations des poissons libérés dans les quatre zones ($P > 0{,}05$). Il ne s'agit que de résultats préliminaires, car l'on s'attend à des retours d'adultes jusqu'en 1991.

Introduction

Several studies have investigated the distribution, abundance, growth, feeding and ecology of juvenile chinook in estuaries of the Pacific Northwest (e.g. Healey 1980; Simenstad et al. 1982; Levings et al. 1986). These results have amassed a substantial base of inferential information, especially food web data, indicating how various chinook stocks use estuaries. These studies have been very useful in formulating strategies for fish habitat management (e.g. CREST 1983; FREMP 1984). However, except for Reimers' (1973) early work on the Sixes River estuary in Oregon, there are no investigations of the importance of estuaries in terms of survival to adults. Reimers' analyses of chinook scale patterns indicated that the life history type that resided in the estuary longest showed the best returns to the spawning population.

Our experiment was designed to provide a new approach to evaluate the importance of the Campbell

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River estuary, on the northeast coast of Vancouver Island, B.C., to chinook survival. The basic strategy was to deprive groups of marked chinook the opportunity to use the estuary. In this way we planned to simulate an estuary that had been completely alienated due to industrial development. For example, if an estuary's wetlands were totally used for harbor facilities, the lower river and estuary would probably be confined and channelized and juvenile chinook might be transported directly by river flows to marine areas without residence in an estuary. We used four marked groups of hatchery chinook (35 000 fish per group) reared at a local hatchery. Fish were released into river, estuary, transition and marine habitats in 1983, 1984 and 1985. In this paper, we present some preliminary results on the survival experiments and accompanying ecological work. Because of the longevity of chinook from Campbell River we expect returns from catches and escapement to continue until 1991. Results presented here are from return data to mid March 1988.

Methods

Methods used in the experimental releases are described in Macdonald et al. (1988); a brief description is given below.

Chinook fry were reared at the Quinsam River hatchery located on a tributary of the Campbell River about 8 km above the estuary. In early April 1983, 1984 and 1985, 140 000 fish (2–4 g) were divided into four groups, marked with coded wire tags and an adipose clip. Each group was then transported by helicopter to release sites in the Quinsam River adjacent to the hatchery (river zone), in the estuary near the mouth of a slough (estuary zone), in a tidal channel on Discovery Passage near the mouth of the Campbell River (transition zone), and at Deepwater Bay, on Discovery Passage about 10 km north of the estuary (marine zone). Surface salinity at the estuary, transition, and marine release sites were approximately 3, 12 and 26‰, respectively. However, considerable variation in surface salinity would be expected with tidal changes at the estuary and transition sites (Levings et al. 1986). Surface temperatures at the time of release were about 10°C in the estuary and transition zones, approximately 9°C at Deepwater Bay, and about 11.5°C in Quinsam River. All groups experienced approximately the same amount of flying time (about 15 min), and were released on April 21, 1983, April 25, 1984, and April 23, 1985.

At each release site, a subsample of fish was obtained from the helicopter bucket. Approximately 50–100 fish were held in each of three cages for observations of short-term mortality, feeding, and stress. At the marine site, observations on fish behavior after release from the helicopter bucket were made by SCUBA divers while at the transition and estuary sites observations were made from the surface by personnel in boats. The dispersion of released fish was tracked by replicate beach seines at stations on the foreshore of the estuary (23 stations) and Discovery Passage (12 stations). All sites, including six additional locations north and south of Deepwater Bay were sampled daily (2–6 samples per station) for one week after the releases occurred. Thereafter, sampling occurred biweekly at the regular beach seine sites until September of each year. Catches were sampled for marked fish. In the laboratory, coded wire tags were removed and decoded and fish from various release groups were measured, weighed and gut contents examined. Data on these topics are reported elsewhere (Macdonald et al. 1988).

Catches of marked chinook in commercial and sport fisheries were monitored by DFO staff through dockside observers at fish plants and creel censuses. Fish returned to the hatchery on Quinsam River were sampled by hatchery staff collecting fish for broodstock purposes. Marked chinook spawning in Quinsam or Campbell River were also recovered by intensive searches using snorkel gear. Data on the recoveries were obtained directly from Quinsam hatchery personnel, as well as the regional Mark Recovery Program (MRP), which has a large data base recording returns of fish and their origin as determined by coded wire tags. Data bases were searched for information to mid-March 1988, and therefore our data are preliminary.

Analyses of these preliminary data on returns from each release zone and release year were conducted using ANOVA on unexpected data. However, the ratios of expanded total returns to observed total returns were tested for differences between release year, return year, and zone using ANOVA and were found to be not significant ($P > 0.05$). Because MRP discards samples for which expansion factors are not available, we actually had slightly more information to work with by using the unexpanded data. Expansion factors were also not applied to escapement data, pending assessment of methods used in the mark/recapture experiments for estimating chinook spawning populations in the Campbell River.

Results

Recoveries of Tagged Fish from Escapement and Fisheries

To date, the majority of released chinook (57.2%) have been returned from fisheries on the north coast of B.C. and Alaska (Fig. 1). Returns from sport fisheries accounted for 39 fish and have been mainly from the vicinity of Discovery Passage. By mid-March 1988, 638 tags had been recovered (Table 1). Zonal survival patterns did not differ between 1983 and 1984 ($P > 0.05$) using χ^2 to test for differences in proportion of fish caught in the 2 years. Data on recoveries

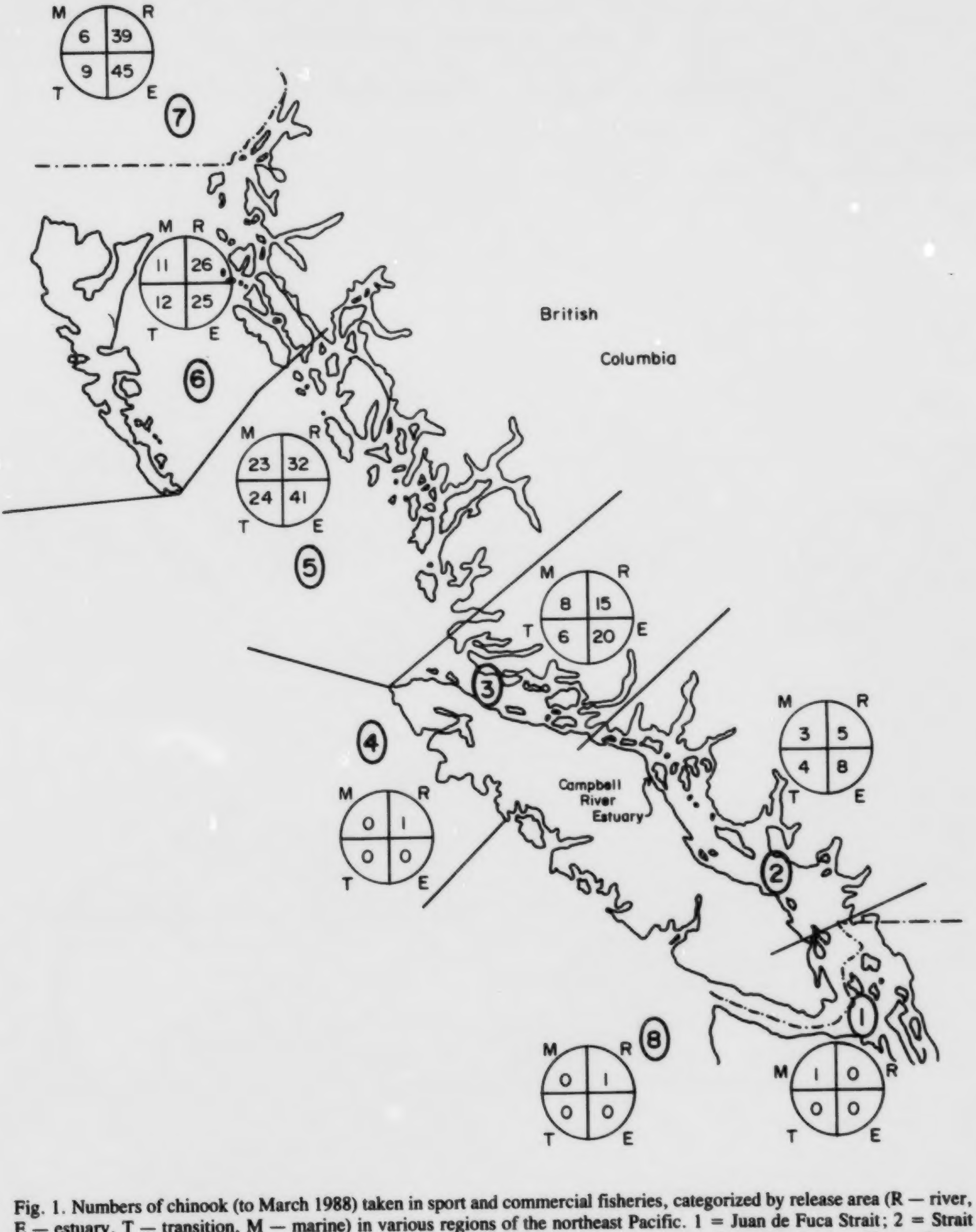
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Fig. 1. Numbers of chinook (to March 1988) taken in sport and commercial fisheries, categorized by release area (R — river, E — estuary, T — transition, M — marine) in various regions of the northeast Pacific. 1 = Juan de Fuca Strait; 2 = Strait of Georgia; 3 = Johnstone Strait; 4 = West Coast Vancouver Island; 5 = Queen Charlotte Sound; 6 = Hecate Strait; 7 = Alaska; and, 8 = Washington Coast.

TABLE 1. Observed tag returns in catch and escapement to mid-March 1988, categorized by release site and year of releases.

Release year	Recovery	River	Estuary	Transition	Marine
1983	catch	69	86	22	15
	escapement	73	78	22	12
	total	142	164	44	27
1984	catch	20	36	9	9
	escapement	17	22	6	4
	total	37	58	15	13
1985	catch	28	18	24	29
	escapement	9	11	13	6
	total	37	29	37	35

TABLE 2. Percentage of tags recovered, categorized by zone and years of recapture.

Released	Recovered	River	Estuary	Transition	Marine	*n*
1983	1984	39.1	39.1	13.0	8.7	23
	1985	32.8	48.3	15.5	3.5	58
	1986	36.3	42.8	11.9	9.0	201
	1987	43.2	43.2	8.4	5.3	95
1984	1985	28.6	57.1	9.5	4.8	21
	1986	28.2	48.7	15.4	7.7	39
	1987	31.8	42.9	11.1	14.3	63
1985	1986	28.6	16.7	28.6	26.2	42
	1987	26.0	23.0	26.0	25.0	96

of fish released in these two years suggest that survival from the different zones decreased in the following order: estuary, river, transition, and marine (ANOVA on log transformed numbers $P < 0.01$). The difference between returns from the river and estuary releases was not significant ($P > 0.05$) for the 1983 release, but marginally so for 1984 ($P = 0.059$). Returns from the transition and marine releases did not differ significantly in either 1983 or 1984 ($P > 0.05$).

The zonal pattern of relative survival for the 1985 release differed significantly (χ^2, $P < 0.01$) from that of the first two release years. There were no significant differences in survival among zones (ANOVA, log transformed numbers, $P > 0.05$). Returns from the estuary release were less than for the other zones, but not significantly so ($P > 0.05$).

Because the numbers of tags put out were very similar for each year and release zone, the observed tag returns provide an index of relative survival. As tag returns are not yet complete, comparisons are based on the first 2 years of recapture for each release year. Returns of tags released in 1984 were about 25 % less that for 1983, but the difference was not significant (ANOVA; $P > 0.05$). Total returns from the 1985 experiment exceeded those from 1983 by 70 % ($P < 0.01$) and those from 1984 by about 2.3-fold ($P < 0.01$). The overall increase in survival of the 1985 release resulted from a marked change in the survival of the transition (3.7-fold, $P < 0.01$) and marine releases (8.8-fold, $P < 0.01$). The difference between the survival of 1985 river release and those of the first 2 years was marginally insignificant ($P = 0.061$). For the estuary this difference was not significant ($P > 0.05$).

Analyses were conducted with returns from each of the release years to investigate the possibility that fish released to the marine and transition sites were improperly imprinted on Campbell and Quinsam River water. If so they could have strayed more on returning to the rivers and could be underrepresented in escapement relative to catch. Because of the apparent difference in survival between years, each year was tested separately by χ^2 on proportions. The differences in zonal proportions between catch and escapement for the 1983 and 1984 releases were not significant ($P > 0.05$) but were marginally insignificant ($P = 0.06$) for the 1985 release. Although results therefore, suggest that straying may have been significant factor for the 1985 release year, the same general pattern in survival was observed whether catch or escapement data were used in each separate year. Straying may therefore not be a significant factor biasing our results.

The patterns of zonal survival did not differ significantly with year of return (Table 2; $P > 0.05$). This suggests that the relative survival patterns were established in the first year after release.

Using data from all return years, the number of fish originating from each release site did not differ significantly between the catch areas to the south and north end of Vancouver Island (Fig. 1) (χ^2; $P > 0.01$). This indicates the catchability of the adult chinook was not influenced by release zone.

Because of the varying age of fish returned from the fishery or from escapement there is an obvious size difference between release years. These were no significant differences in fish length with respect to release location for fish released in 1983, 1984 or 1985 ($P > 0.05$).

Discussion

Factors Influencing Survival

Four assertions are commonly made with references to marshes (often thought of as synonymous with estuaries) and their importance to young salmon (Dorcey et al. 1978): estuaries are temporary residence areas; estuaries are seawater acclimation areas; estuaries are rich feeding areas; estuaries are refugia from predators. Detailed, site-specific observations of fish distribution, feeding and predation would be required to provide the ecological data needed to interpret differences in survival that were observed between the groups in the context of the importance of estuaries. Limited data were obtained (Macdonald et al. 1988) and our comments on these topics are therefore largely speculative.

Macdonald et al. (1988) have shown that the use of the Campbell River estuary by the chinook released there and in the river was prolonged. Some fish released at the transition site returned to the estuary, but very few from the marine site. Residency estimates were in the order of 25 to 50 d, comparable to estimates obtained for chinook fry in the Fraser River estuary (Levy and Northcote 1982) and in the Nanaimo River estuary (Healey 1980). Estuary residency in 1983 and 1984 appeared to confer benefits on chinook in terms of survival to catch and escapement, but this was not the case for the 1985 releases. While the combined river and estuary returns differed little between the three release years, there was a significant difference ($P<0.01$) in combined returns from the 1985 marine and transition releases when compared to 1983 and 1984. It appears that there was a marked improvement in marine survival conditions outside the estuary in 1985. Obviously the annual differences in interactions between conditions in the estuary and marine habitats have to be considered in any appraisal of survival in various life stages. A longer time series is required to quantify inter-annual changes in relative survival of the four release groups.

With respect to osmoregulation or seawater acclimation concerns, our experimental fish were apparently "ready for sea", as they passed a seawater challenge test before release (Macdonald et al. 1988). As well their average weight was over 1.5 g which according to Clarke and Shelbourne (1985) is a threshold size above which chinook can tolerate change from freshwater to 30‰. Short-term results verified this, as mortality in groups held in cages at the marine sites was variable but low. Mortality at the marine cage site was approximately 10 % in 1985, but this was attributed to handing mortality, as described in Macdonald et al. (1988). In other years the mortality in cage-held fish was <5 %. There was limited direct mortality after releases from the helicopter bucket at Deepwater Bay, as observed by SCUBA (Macdonald et al. 1988). However if smaller fish, for example wild fry, were transferred directly to seawater, mortality would be higher and growth reduced, at least as indicated by the laboratory experiments of Kepshire and McNeil (1972). In their experiments, chinook fry raised in seawater (33‰) grew at $2.1\,\%\ \mathrm{d}^{-1}$ compared to $2.7\,\%\ \mathrm{d}^{-1}$ for fish in brackish water (17–18‰). Therefore, although our experiment did not test directly for osmoregulatory effects, exposure to brackish water habitat is probably important for the survival of wild fry and small hatchery chinook. Future experiments should also test for effects of migration on osmoregulatory ability, since Zaugg et al. (1985) found that the ability of chinook smolts to tolerate seawater was enhanced by migration through the Columbia River.

Evidence concerning the importance of the Campbell River estuary for chinook feeding is equivocal. The density of potential epibenthic food organisms is higher outside the estuary than within it (Kask et al. 1986). By May and June the estuary is used extensively by wild and hatchery chinook (Levings et al. 1986). In 1985, mean size of wild chinook fry in the estuary was 66 %, and maximum size 31 % of the values for 1983 and 1984 ($P<0.01$). This may have been associated with the much greater total numbers of juvenile salmon in the estuary, which were five to eight times more than in 1983 and 1984. A similar decrease in growth also occurred in the experimental chinook released to the river and the estuary (C.D. McAllister, unpublished data; Pacific Biological Station, Nanaimo, B.C. V9R 5K6). Diet analyses reported elsewhere by Macdonald et al. (1988) did not suggest any evidence for food limitation using "forage ratio" data from both free-ranging and caged fish from estuary, transition, or marine release zones but caged fish in the river area ate less food. Evidence for food limitation has been presented by Nielsen et al. (1985) for juvenile chinook in the Sixes River estuary in Oregon. Other work at the Campbell River estuary on wild chinook (Levings et al. 1986) indicated that growth rates there were lower than those observed at the Nanaimo estuary (Healey, 1980) so perhaps juvenile chinook in the Campbell River estuary are indeed limited by food.

Predation is thought to be a major factor influencing juvenile salmon from survival in the coastal zone (Healey 1979) and may operate via different agents and at different rates in the four habitats we released our fish into. Data allowing comparison of predation on juvenile salmon amongst different times and places are exceedingly rare. Our own preliminary observations (Macdonald et al. 1988) and some data from other studies suggest that the potential for predation may differ between shallow estuaries and the deeper coastal seaways such as Discovery Passage. It seems likely that shallow and vegetated areas in estuaries and shore zones could provide refuges from larger predatory fishes, and that such fishes could operate more successfully in the deeper channels. Hvidsten and Mokkelgjerd (1987), for example, found that Atlantic cod (*Gadus morhua*) were major predators on Atlantic salmon smolts (*Salmo salar*) in a Norwegian fjord setting similar to Discovery Passage. Similarly, predation by diving birds might be restricted in shallow vegetated areas. However, some birds such as mergansers (*Mergus merganser*) are known to be successful predators on hatchery coho smolts in small streams (Wood 1987). Mace (1983) estimated that Bonaparte's gulls (*Larus philadelphia*) at the nearby Big Qualicum estuary, a narrow channelized water body, consumed about 8–10 % of newly-released hatchery chinook using that estuary in daytime. We were unable to quantify predation by fish or birds during out experiments, but field observations on the day our fish were released showed that Bonaparte's gulls were more abundant at the marine release site compared to the other three locations. An exception was 1985, when they were relatively abundant at both the transition and marine release sites.

Limitations of Experimental Design: Time of release and size considerations

Some aspects of time and size of release and effects on survival must be taken in to account in assessing the results of this experiment. We would have preferred to conduct the work using smaller wild fish, but sufficient numbers were not available for this purpose, and the size of fish from the hatchery could not be reduced by manipulating water temperature or rations. As a result our experimental chinook were about 2.5 g larger that wild fry using this estuary in late April, which are between 0.5 and 0.8 g at this time (Levings et al. 1986). However, our fish were similar in size to the chinook "yearling riverine smolts" (2.4 g; Carl and Healey 1984) that move to the Nanaimo estuary in early May (Healey 1980). Residency time for chinook fry at the Campbell River estuary appears to be inversely related to size (Levings et al. 1986), but subsequent survival to adult may be directly related to fish size (Bilton1984). Given size-dependent mortality, we suggest that the survival of the experimental chinook should have been greater than that of the wild fry.

Beach seine catches of wild chinook at Deepwater Bay, the site of the marine releases, peaked in late June and early July (Levings et al. 1986) about two months later than the time of our experimental releases. Migrating wild chinook fry arrive in this area after the numbers of juvenile salmonids, chiefly pink and chum salmon, have peaked but densities of the latter two species were still higher than in late April. Wild chinook salmon weighed 4 to 5 g on arrival in late June in the marine release area, and were considerably larger than the experimental chinook at the time of release. Assuming that mortality was size-dependent, the survival of normally migrating wild chinook fry, subsequent to their arrival in Deepwater Bay, should have been greater than that of the experimental release. This difference could have been larger if lower numbers of accompanying pink and chum at the time of the experimental release in April had reduced prey buffering. However, the direct transport of fish from the hatchery to Deepwater Bay bypassed sources of mortality that the other releases encountered in the river, the estuary and southern Discovery Passage. These factors in the experimental design suggest that we may have over-estimated the survival benefit conferred by estuary residency experienced by wild chinook fry, except for osmoregulatory concerns, discussed above.

Concluding Discussion

If results of future experiments do confirm or even quantify the benefits of estuary residence, and its variability within and between systems, we will still need to know the causes, if we are to manage estuarine habitat, and also stock densities in relation to rearing capacity. While our results demonstrate that estuary residence conferred a substantial survival benefit to the experimental fish released there in 2 out of 3 years, application to wild chinook fry remains somewhat speculative. The mean individual residence time of wild chinook fry in the Campbell River estuary has been estimated as three to six weeks (Levings et al. 1986), similar to that for the Nanaimo River estuary (Healey 1980). In the Campbell estuary, the chinook fry maintain residency despite a very large tidal prism, strong river currents, and little likelihood of returning if swept out. In addition, the evidence to date suggests that availability of preferred foods may be less inside the Campbell River estuary. This suggests that the binding is very strong. However, our information on the proportions of the stock not using the estuary, by chance or behavior, is weak. Thus, even if survival of fry using the transition zone is lower it is possible that a large fraction of the fry returning as adults originate from fry with short estuary residence times. This suggests a need for research to quantify residents and non-residents.

In addition to natural variability in estuarine habitats, cultural changes must also be taken into account. Most of the estuaries logistically convenient for study have already been heavily modified, and are subject to continued development. The Campbell River estuary is an example. About 80 % of the shoreline is encumbered by rip rap, log storage, urban development, and marine facilities. The channel bottoms are regularly disrupted by towed log rafts and propeller scour. Habitat reclamation is another "disturbance" (Brownlee et al. 1984) which will not reach a steady state for some time to come. Proposals for major dredging are being considered. It seems unlikely that such cultural changes can be subject to experimental control. Thus statistical control requiring years of observation may be necessary. In addition, research focussing on the processes controlling survival is necessary if the essential or desirable habitat factors are to be identified and managed. Although important, it is insufficient to know that estuaries confer some average survival advantage. For example, if the advantage is confirmed, and it is found to result from salt water acclimation, the implications for management are different than if production of preferred foods is responsible.

Despite the uncertainties discussed above, we feel that the recent results tend to confirm other studies supporting the position that estuaries should be managed to conserve and improve estuarine habitats for chinook production.

Acknowledgments

This study was developed through discussions with the late F.C. Withler and we are indebted to him for this help. Thank are also due to Jim Van Tine,Manager of the Quinsam hatchery, for rearing chinook for use in the experiments. A number of students, term employees and job creation personnel assisted with the field and laboratory work.

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Differential Survival of Grays Harbor Basin Anadromous Salmonids: Water Quality Implications

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Abstract

SEILER, D. 1989. Differential survival of Grays Harbor basin anadromous salmonids: water quality implications, p. 123–135. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Coded wire tagging experiments were conducted utilizing Grays Harbor wild and hatchery coho salmon (*Oncorhynchus kisutch*) over four broods (1980–83). Results demonstrate that Chehalis River coho smolts survive to adult recruitment at one half the rate of coho smolts from the nearby Humptulips River. Low survival of wild coho has resulted in under escapement in the Chehalis River in 3 of the last 5 yr despite severe harvest restrictions. These results have serious implications for other Chehalis River anadromous salmonid stocks. Poor post smolt survival prevents realization of substantial fish production potential and results in a major resource loss that exceeds one million dollars per year. Historically, severely degraded water quality in inner Grays Harbor, caused by pulp mill discharges, seriously impacted anadromous salmonid stocks. Despite significant improvements in effluent treatment, impaired water quality remains the most probable cause of continued low survival. A state funded, cooperative study involving industry, universities and various county, state and federal agencies is currently investigating the cause(s) of poor survival.

Résumé

SEILER, D. 1989. Differential survival of Grays Harbor basin anadromous salmonids: water quality implications, p. 123–135. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Des expériences de marquage au fil de fer codé ont été effectuées avec des saumons cohos (*Oncorhynchus kisutch*) sauvages et d'élevage de quatre générations (1980-1983) dans le havre Grays. Les résultats démontrent que le taux de survie jusqu'au recrutement à l'âge adulte des smolts de coho de la rivière Chehalis ne représente que 50 % de celui des smolts de coho dans la rivière Humptulips, située à proximité. En raison du faible taux de survie des cohos sauvages, les échappées ont aussi été faibles dans la rivière Chehalis pendant trois des cinq dernières années, en dépit des restrictions de capture rigoureuses. Ces résultats laissent présager de graves répercussions pour d'autres stocks de salmonidés anadromes de la rivière Chehalis. Le faible taux de survie pendant la période de post-smoltification réduit considérablement le potentiel de production piscicole, ce qui se traduit par une importante perte de ressources, représentant plus d'un million de dollars par année. Au fil des ans, la forte dégradation de la qualité de l'eau au centre du havre Grays, causée par les rejets des usines de pâtes, a fortement perturbé les stocks de salmonidés anadromes. En dépit de nettes améliorations apportées au traitement des effluents, la piètre qualité de l'eau demeure la cause la plus probable du faible taux de survie qui persiste. Une étude conjointe subventionnée par l'État à laquelle collaborent l'industrie, les universités et divers pays ainsi que des organismes de l'État et du Fédéral est actuellement en cours pour déterminer les causes du faible taux de survie.

Introduction

Low adult returns of coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon and steelhead trout (*Salmo gairdneri*) to the Chehalis River have been evident for over 50 years. While these stocks have been impacted by overfishing and habitat degradation resulting from logging, agriculture, gravel mining and other development, the particularly poor returns to this system have long been blamed on pollution in inner Grays Harbor, the Chehalis River's estuary. Although many investigations into the harbor's water quality conditions have found them to be degraded, specific impact(s) of poor water quality on anadromous stocks has been difficult to quantify.

In 1980, the Washington Department of Fisheries (WDF) initiated long term studies to assess production and survival of wild and hatchery coho stocks within the Grays Harbor Basin. Initially, the primary goal was to improve harvest management efforts, but results soon indicated that poor survival of Chehalis River stocks represented the most serious problem requiring attention.

Findings of this ongoing investigation, relevant to impacts of habitat alteration on fish populations at the stock level, are presented herein. Specific objectives of this paper are to present a brief summary of Grays Harbor's historical water quality and fish survival problems, document and quantify the survival problem that continues to affect Chehalis Basin stocks, demonstrate the productive capacity of this watershed, estimate the cost of the poor survival and draw some conclusions from the history and current status of this resource problem that may pertain to similar situations elsewhere.

Study Area

Grays Harbor, located on the Washington coast, receives the runoff from a 6605 km^2 watershed and is the fourth largest coastal estuary in the western United States. The Chehalis River and its lower tributaries enter the harbor at its east end (Fig. 1) and together, comprise the largest watershed (5709 km^2) in the State of Washington outside the Columbia River system. The other major tributary to Grays Harbor is the Humptulips River which drains 635 km^2 and enters the harbor at its northwest end (Fig. 1). The lower Chehalis River and inner Grays Harbor is heavily populated, industrialized, frequently dredged and receives the discharge of three municipal sewage treatment plants and the treated effluent of two sulfite pulp mills. Conversely, the Humptulips River and it's estuary at North Bay remain undeveloped. Consequently, water quality conditions at the terminus of each river are very different. This major difference between the two systems has been the basis for utilizing anadromous fish production of the Humptulips River as a natural control against which the status of Chehalis Basin stocks can be compared.

Background and Problem Documentation

Water Quality History

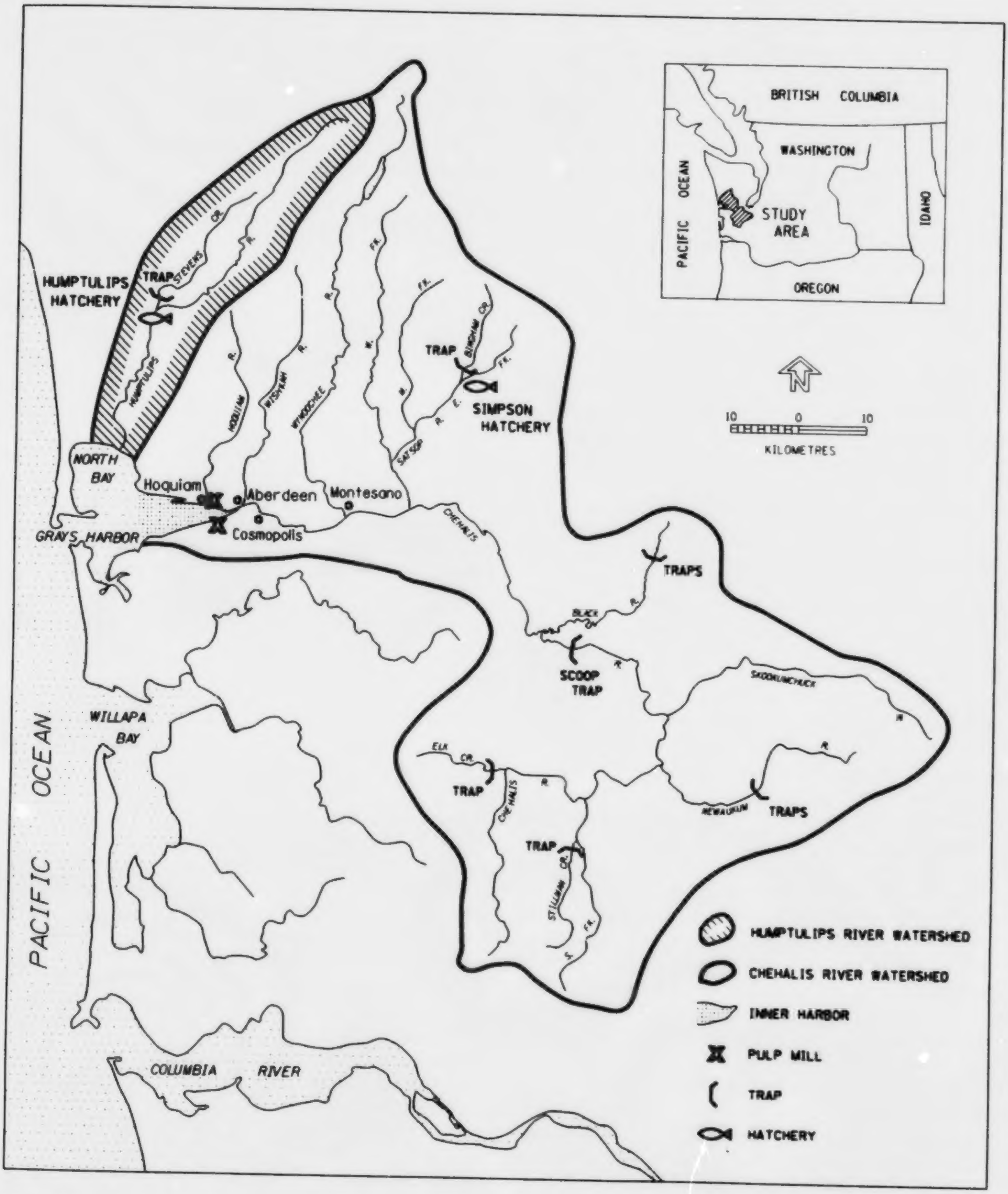
Recurrent fish kills in inner Grays Harbor during the 1930's prompted the State of Washington Pollution Control Commission to thoroughly investigate the cause. Extensive field sampling conducted between 1937 and 1939 revealed that low dissolved oxygen (DO) concentrations (often near zero) in inner Grays Harbor during low flows (May–October) caused the fish kills (Eriksen and Townsend 1940). These conditions resulted from the untreated waste of one 227 t/d sulfite pulp mill. Located near the mouth of the Hoquiam River, this mill which began operation in 1928, exerted a biochemical oxygen demand (BOD) of 115.2×10^3 kg/d. This load is roughly equivalent to the raw sewage from 1.4 million people. Impacts of effluent are most severe during low flows as flushing is reduced. Estimates of flushing rates of the inner harbor during low flows have ranged from 21 d (Beverage and Swecker 1969) to 42 d (Eriksend and Townsend 1940).

Water quality in inner Grays Harbor, as indicated by DO, remained severly degraded into the 1950's (Peterson et al. 1957). Some improvement was achieved, beginning in the late 1940's, by impounding pulp mill effluent during the low flow period for discharge when the freshwater input to the inner harbor exceeded 71 m/s (Orlob et al. 1951). However, in 1957, a second sulfite pulpmill (363 t/d) began operation. Together, these two mills discharged an average BOD of 209×10^3 kg/d (124×10^3 kg/d during low flows when effluent was stored, to over 260×10^3 kg/d during the winter when the stored effluent was released) (McCall 1970). In 1965, McCall estimated that wastes from the pulp and paper industry comprised over 94 % of the total (natural and man imposed) BOD load to inner Grays Harbor.

By the mid 1970's, both pulp mills were required to install secondary treatment plants, resulting in a significant decrease in BOD (to 18×10^3 kg/d). Although DO levels increased as a result, average DO in inner Grays Harbor during the summer was not consistently above the 5 ppm standard set by regulation until the early 1980's (Washington State Deptartment of Ecology (WDOE) unpubl. data).

Before DO concentrations increased to the minimum levels required for aquatic life, effluent toxicity was largely ignored. Early investigators acknowledged that the volumes of sulfite waste liquor discharged to the harbor could result in conditions toxic to salmonids (and other fish) especially during low flows but the oxygen depletion resulting from those effluents would surely kill fish first (Eriksen and Townsend 1940). However, as progress was made on reducing the BOD load to the harbor, toxicity of effluents was questioned.

In 1980, renewal of the pulp mills' National Pollution Discharge Elimination System permits (U.S. Water Pollution Control Act 1972) contained a provision to monitor effluent toxicity on a quarterly basis. A 96-h static test using rainbow trout in a 65 % solution of effluent (neutralized to pH of 6.5–8.0) in fresh water (DO $>$ 7 ppm) was developed. Permit conditions require an 80 % survival rate. According to reports sub-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WILLAPA BAY
PACIFIC OCEAN
COLUMBIA RIVER
HUMPTULIPS RIVER WATERSHED
CHEHALIS RIVER WATERSHED
INNER HARBOR
PULP MILL
TRAP
HATCHERY

FIG. 1. Grays Harbor study area showing relative size and location of the Chehalis and Humptulips rivers, major tributaries, smolt trapping sites, hatcheries, pulp mills and cities.

mitted by each mill, one nearly always achieves 100 % survival while survivals at the other mill have ranged from zero to 100 %. In recent years, the bioassay failures at the one mill have occured most in the spring. This mill has been ordered to conduct the bioassay more frequently and to determine the source of the mortality. Two investigations have been conducted. The first was inconclusive and the second resulted in some operational changes that may have reduced effluent toxicity as evidenced by improved bioassay results in spring 1987 (WDOE unpubl. data).

Fishery Observations

Harvest and escapement information for Grays Harbor chinook and coho demonstrates that the Humptulips River has consistently received higher returns of these species, relative to its size, than the Chehalis River system. Deschamps and Johnson (1957) estimated that 40 % of the chinook and 28 % of the coho catch in Grays Harbor originated from the Humptulips River. On the basis of watershed area, the Humptulips River should produce about 10 % of the total catch of chinook and coho in the harbor. Differential quality of stream habitats do not explain these discrepancies as the freshwater environment in the Chehalis system is equal to or superior to that of the Humptulips River. In fact, the Chehalis River system includes more tributaries in proportion to its watershed area than the Humptulips, making it decidedly better suited to coho production (Phinney and Bucknell 1975). This disparity between salmon returns to the two rivers has continued through the present. For example, the Humptulips River has accounted for an average of 33.6 % of the total chinook to Grays Harbor over the last 17 years (WDF unpubl. data).

Although data on steelhead are not as extensive as for chinook and coho, the available information demonstrates that adult steelhead returns to the Chehalis River have also been low relative to those of the Humptulips River. Peterson et al. (1957) documented that releases of fin-marked hatchery steelhead trout in the Humptulips River produced adults whereas groups released into several lower tributaries of the Chehalis River failed to produce adult returns. They attributed these disparate results to an "unfavorable estuarial environment". Over the last 11 winter steelhead fishing seasons for which data are available (through 1984–85), the Humptulips River has accounted for an average of 47.2 % of the combined sport and commercial catch of hatchery and wild steelhead in the Grays Harbor Basin (QFD and WDG 1986). Additionally, estimates of wild steelhead catch and escapement for 1983–85 place the contribution of the Humptulips River to the total Grays Harbor production at 32.9 %.

Unlike chinook, coho, and steelhead, chum salmon (*O. keta*) production is not lower from the Chehalis River as compared to that of the Humptulips River. This lack of difference has been attributed to earlier emigration of juveniles which occurs while river flows are higher and consequently while water quality in the inner harbor is better (Eriksen and Townsend 1940;Peterson et al. 1957). Conversely, these investigators also concluded that the inner harbor's adverse water quality most severly impacted chinook stocks due to their later emigration and extended use of the estuary during the low flow period of "acute pollution".

Comparison of the harvest records for the commercial gillnet fisheries on Grays Harbor coho and chinook to those of Willapa Bay (Fig. 1), an estuary to the south with notably good water quality, provided additional evidence that survival through inner Grays Harbor was poor. Willapa Bay's 2200 km^2 watershed (one third the size of Grays Harbor's), is drained by four relatively small river systems, yet fishery records indicate that from the mid 1920's to the mid 1950's, this system produced about the same level of terminal area chinook harvest as Grays Harbor (Peterson et al. 1957). Over the same period, the number of coho caught in Willapa Bay's gillnet fishery was about 50–75 % of Grays Harbor's, but again, far higher than habitat quantity would predict. These harvest levels are especially significant when the generally lower quality of the Willapa Basin's stream habitat is considered (Phinney and Bucknell 1975).

Attempts to Link Poor Fish Survival to Pollution

The above comparisons provide substantial empirical evidence that Chehalis Basin chinook and coho salmon and steelhead survived to adults at fractions of the rates of fish of the same species from neighboring river systems; systems without a polluted estuary. To more definitively quantify the impact of poor water quality in inner Grays Harbor on fish survival, WDF implemented the first of two fin-mark experiments in 1966. Equal groups of 1964 brood coho smolts (200 000 per group), reared at Simpson Hatchery (SH) (Fig. 1), were differentially fin-marked. (The term smolt, used herein, refers to yearling coho.) One group was released into the Satsop River (Fig. 1) and the other was transported and released into the Humptulips River at a distance from the estuary equal to that of the group released into the Satsop River. The identical experiment was repeated in 1967 with 1965 brood smolts. The groups released into the Humptulips River contributed to fisheries in 1967 and 1968 at 1.5 and 2.7 times, respectively, the groups released into the Satsop River (Wright and Bernhardt 1969; Wright 1970). These rates underestimated the actual survival difference because the groups released into the Humptulips River were subjected to additional transport stress. We now estimate that transfer of coho smolts (via tank truck) and release into a different watershed may reduce survival to adults by up to 50% or more (WDF unpubl. data). Correction of the groups released into the Humptulips River by this factor would result in an average difference in survival of four times. To many, the results of these experiments affirmed the "pollution block" theory; that severe pollution in the inner harbor was causing the low returns of fish to the Chehalis River (Deschamps and Senn 1969).

To more directly investigate the effects of pollution in inner Grays Harbor on juvenile salmon, the WDF conducted live box studies from June to August of 1969 and 1970 (Deschamps and Phinney 1971). On five occasions in 1969 and three in 1970, 20 chinook fingerlings were placed in five live boxes that were located upstream and downstream of the pulp mills. Results demonstrated that mortality was directly related to proximity to the pulpmills and with operation of the mills. The station closest to the pulp mills had 100% mortality within 16 h while the mills were operating, whereas the station farthest upstream of the mills (located in the mouth of the Wishkah River) had the lowest mortality during operation of the mills (20–40% after 22 h) and zero mortality after 22 h when the pulp mills were not operating. DO levels during these studies generally were above the then minimum standard of 4.5 mg/L. Deschamps and Phinney concluded that a toxic condition existed in the inner harbor and strongly implicated pulp mill discharges as the cause.

To verify these studies and to measure the change in water quality resulting from some improvements in waste water treatment that had been made at the pulp mills, WDOE conducted in situ live box studies on three occasions in 1972 (June 28, July 5 and August 9). Methods and locations were nearly identical to those employed in the 1969 and 1970 studies. While mortality remained high, results indicated that toxicity had decreased, from 97 to 67%. This improvement was attributed to the new waste water treatment facilities (Jeane 1973).

Results of these studies increased the pressure to correct the pollution problem in the inner harbor. In response, the pulp industry, in 1974, proposed a second joint agency-industry study to investigate water quality in Grays Harbor and its effect on juvenile salmonids. Participants included the Weyerhauser Company, ITT Rayonier, WDOE and WDF. An earlier cooperative study, conducted from 1964 to 1966 (but not reported until 1971) concluded that "the water quality in Grays Harbor must be improved if the aquatic resources of the area are to be protected and enhanced" (WDF 1971). This study failed, however, to accomplish a major objective of evaluating the effect of the water quality on aquatic organisms.

In the second series of cooperative studies, in situ bioassays were performed with chinook and coho in conjunction with water quality monitoring. While mortality in the live box tests in the inner harbor decreased when the pulp mills shutdown for four days, some of the mortality observed during plant operation also was attributed to disease (vibrio), naturally poor water quality, physiological stress from capture and handling, and the live box design. Consequently, results of the bioassays were judged inconclusive by industry. Agency investigators maintained that "effluent toxicity appeared to be a causative factor in the live box mortalities based on the fact that mortalities decreased during the shutdown of the pulp mills" (WDOE 1974). Despite the preponderance of other evidence indicating poor fish survival, the disparate interpretations of the results of these studies served to defuse the pollution block theory.

In June 1973 (just prior to the second cooperative investigation), WDF conducted a coded wire tagging experiment (Jefferts et al. 1963) utilizing fall chinook to further assess survival through the inner harbor. Two groups of 1972 brood fall chinook (100 000 per group), were reared at SH and tagged. One group was released from SH and the other was transported and released in the Humptulips River. The latter group contributed to ocean fisheries at 18 times the group that emigrated through inner Grays Harbor (Fuss et al. 1981). As with the earlier coho fin-mark experiments, if transport stress was accounted for, this difference would be even greater.

The outcome of this experiment, however, received little attention, because by the time results were available (1979), major advances in wastewater treatment, as required by the U.S. Environmental Protection Agency, had been implemented. While past pollution problems were acknowledged, it was widely assumed that the advances in effluent treatment had resolved the survival problem. Verification of this assumption, however, was delayed.

Methods

In 1980, the WDF's Freshwater Production Evaluation Program, a long-term research project designed to improve management of naturally spawning salmon stocks, was expanded to include a coastal station (Seiler et al. 1981 and 1984). Directed primarily at coho, this program's basic study plan involves enumeration of adult escapement and resultant smolt production via upstream and downstream migrant trapping, respectively. Survival from smolts to adult recruitment is measured by coded wire tagging. Harvest is estimated through existing coastwide ocean and terminal fisheries sampling programs (PMFC 1982). Escapement is measured by returns of tags to the upstream trapping facilities.

Bingham Creek, a tributary to the East Fork Satsop River (Fig. 1), was selected as the coastal study stream because an existing barrier dam and fishway trap provided the means to enumerate escapement. In 1981, an 100 % efficient downstream migrant trapping facility was constructed at the barrier dam. Upstream trapping began in 1980 and downstream enumeration and tagging began in 1982.

To supplement the information collected at this station, and also to provide a measure of production and survival from the Humptulips River, temporary smolt traps (Blankenship and Tivel 1980) were operated on tributaries to the Chehalis and Humptulips rivers beginning in 1982 (Fig. 1). Coho smolts captured at these traps were also tagged each year beginning in 1982 (Table 1). Beaver and Waddell Creeks are tributaries to Black River.

In addition, coho smolt production from the upper Chehalis Basin (2383 km^2) was measured in 1986. A floating inclined plane screen trap (scoop trap) (Seiler et al. 1981) was operated throughout the spring migration on the Chehalis River upstream of the confluence of the Black River (Fig. 1). All coho smolts captured in this trap were examined for the presence of an adipose fin. Recaptures of adipose marked coho smolts, released from the traps on the tributaries upstream of the scoop trap, provided the means to estimate total smolt production (Seiler et al. 1984).

Concurrent with trapping and tagging wild coho smolts, representative groups of SH and Humptulips Hatchery (HH) coho smolt production were coded wire tagged each year beginning with the 1980 brood (Table 2, Fig. 1). To assess the stock performance of offstation releases (hatchery production transported and released into streams other than that on which the hatchery is located — also referred to herein as outplants) of coho smolts into the Chehalis River system, a portion of these releases were also tagged each year.

In 1985, a separate coded wire tagging experiment was initiated with 1983 brood HH coho smolts to assess survival through inner Grays Harbor and estimate transport mortality. Three identically cultured groups of coho were coded wire tagged. One group was transported and released into tributaries of the lower Chehalis River (Fig. 1). As a control for this group, a second group was loaded into planting trucks at the same density and then transported in a circle for the same duration (1.5 h) as the outplanted group before release at the hatchery's outfall. As a control for the second group, a third group was simply released from the hatchery on the same day in the normal manner.

All 1983 brood hatchery groups were tagged with replicated tag wire, an innovation that allows direct calculation of variances.

Ocean contribution was used as an index of survival for all comparisons between Chehalis and Humptulips River stocks. This was neccessary since on return, separation of stocks occurs within Grays Harbor resulting in differential harvest in the terminal net fishery as well as the river sport fishery. This would not pose a problem if escapement of tags could be measured for each group. Escapement, however, can only be measured at the SH complex (including the Bingham Creek trap). Differences in contribution rates between the Chehalis River and Humptulips River hatchery and wild tag groups were tested for significance by a paired t-test (Zar 1984).

Results

Over four brood years (1980–83), the contribution rate to ocean fisheries of tagged Chehalis Basin wild coho averaged 50 % of tagged Humptulips River wild coho (Tables 1,3). This difference is significant ($t=3.67$, df=3, $P<0.05$).

Three broods (1980, 1982, 1983) of tagged SH coho contributed to ocean fisheries at an average of 59 % of the same broods of tagged HH coho (Tables 2,3). The difference in contribution rates of these tag groups was not as consistant as those of the wild groups. As a result, with only 3 yr of data, the difference over these years was not significant. In two of the years however, the difference was clearly significant.

Over 4 brood years (1980–83), the tagged hatchery coho smolts outplanted into the Chehalis River system contributed to ocean and harbor fisheries at 18.5 % of the rates of the tagged hatchery coho smolts released at SH (Table 4).

The 1983 brood tagged HH coho transported and released into tributaries of the lower Chehalis River contributed to 1986 ocean fisheries at 0.07 %, the transport control group at 1.51 % and the overall control at 2.01 % (Table 5). These results estimate that outplanting of hatchery coho smolts into and emigration from the Chehalis River reduced survival by over 20 times relative to release and emigration from the Humptulips River. The transport effect was estimated at 24.9 % (1 – 1.51/2.01).

Other important results obtained from these studies that help define the production and survival rates of Chehalis River wild and hatchery coho include the following:

- Over brood years 1980–83, survival from smolt to adult (catch plus escapement) of tagged wild Bingham Creek coho and tagged SH coho has averaged 4.48 % and 2.45 %, respectively (Table 6).
- Production of wild coho smolts from Bingham Creek has averaged 31 000 and smolt production per female has averaged 48.8 smolts (Table 7).
- Production of 1984 brood coho smolts from the Chehalis River upstream of the scoop trap was estimated at 884 000 in 1986.

Discussion

Results of this hatchery and wildstock tagging program demonstrate that, in the 1980's, Chehalis Basin coho stocks have survived from smolt to adult recruit-

TABLE 1. Estimated contribution rates to ocean fisheries of wild Grays Harbor Basin coded wire tagged coho, brood years 1980-83.

Basin/ stream	Tag code	Number tagged	Estimated ocean recoveries (%)					
			CA	OR	WA	B.C.	AK	Total
				1980 Brood				
Chehalis Basin								
Bingham	632358	26040	—	0.07	0.07	1.01	0.05	1.21
Black	632336	5086	—	0.04	0.67	1.26	—	1.97
Beaver	632415	8487	—	0.18	0.46	2.39	—	3.03
Stillman	632548	2744	—	0.18	0.47	2.33	—	2.99
M. New.	632414	3589	—	0.06	0.56	1.78	—	2.40
N. New.	632549	1242	—	0.16	—	0.64	—	0.81
Pooled		**47275**[a]	**—**	**0.09**	**0.26**	**1.41**	**0.03**	**1.80**
Humptulips Basin								
Stevens	**632357**	**11063**	**—**	**0.14**	**0.33**	**3.07**	**0.05**	**3.59**
				1981 Brood				
Chehalis Basin								
Bingham	632726	23824	—	0.04	0.04	0.78	0.02	0.87
Black	632230	9382	—	0.09	—	1.00	0.07	1.16
Black	632728	32013	—	0.13	0.07	1.20	0.05	1.45
Stillman	632418	5844	—	0.09	—	0.72	0.05	0.86
Newaukum	632559	7599	—	0.04	0.20	0.66	—	0.89
Pooled		**78662**	**—**	**0.08**	**0.06**	**0.96**	**0.04**	**1.14**
Humptulips Basin								
Stevens	**632719**	**20578**	**—**	**0.18**	**0.07**	**1.81**	**0.07**	**2.13**
				1982 Brood				
Chehalis Basin								
Bingham	633027	31602	—	—	0.05	0.30	—	0.35
Beaver	633046	10760	—	—	0.06	0.54	—	0.60
Beaver	633061	10717	—	—	0.02	0.27	—	0.29
Beaver	633062	7663	—	—	—	0.10	—	0.10
Black	633047	20910	—	0.01	0.20	0.61	—	0.82
Black	632453	7424	—	0.05	—	0.09	—	0.14
Stillman	632547	9166	—	0.10	—	0.31	—	0.41
Newaukum	632910	10272	—	0.07	0.18	0.18	—	0.43
Elk	632911	858	—	—	—	—	—	—
Pooled		**109372**	**—**	**0.02**	**0.06**	**0.34**	**—**	**0.44**
Humptulips Basin								
Stevens	633048	18055	—	0.07	0.14	0.68	—	0.88
Stevens	633107	4415	—	0.05	0.23	0.20	—	0.48
Pooled		**22470**	**—**	**0.06**	**0.16**	**0.58**	**—**	**0.80**
				1983 Brood				
Chehalis Basin								
Bingham	633035	21369	—	0.06	0.04	0.71	—	0.81
Waddell	633209	4830	—	—	0.04	0.62	—	0.66
Beaver	633423	23998	—	0.06	0.05	0.85	—	0.96
Black	633425	28142	—	0.03	0.05	1.45	0.01	1.54
Newaukum	633444	10942	—	—	0.02	1.06	—	1.08
Stillman	633443	7242	—	—	0.03	1.13	—	1.16
Pooled		**96523**	**—**	**0.04**	**0.04**	**1.03**	**—**	**1.11**
Humptulips Basin								
Stevens	633424	21914	0.01	0.13	0.14	2.19	0.01	2.48
Stevens	633010	3530	—	0.48	0.14	3.26	0.11	3.99
Pooled		**25444**	**0.01**	**0.18**	**0.14**	**2.34**	**0.03**	**2.69**

[a] Includes 87 smolts tagged at Waddell Creek; none of these were recovered.

TABLE 2. Estimated contribution rates to ocean fisheries of Grays Harbor Basin hatchery coded wire tagged coho, brood years 1980–83.

Hatchery	Tag code	Number tagged	Estimated ocean recoveries (%)					
			CA	OR	WA	B.C.	AK	Total
				1980 Brood				
Simpson	632408	52465	—	0.03	0.05	0.62	—	0.70
Humptulips	632404	51468	—	0.15	0.31	1.45	—	1.91
				1981 Brood				
Simpson	632647	47734	—	0.13	0.04	1.07	0.01	1.25
Humptulips	—[a]							
				1982 Brood				
Simpson	632861	45404	—	0.01	0.08	0.41	—	0.50
Humptulips	632744	48010	—	0.04	0.06	0.39	—	0.49
				1983 Brood				
Simpson	633345	25982	—	0.03	0.05	1.00	0.05	1.13
Simpson	633346	25337	—	0.07	0.02	0.99	—	1.08
Pooled		**51319**	**—**	**0.05**	**0.03**	**0.99**	**0.03**	**1.10**
Humptulips	632817	16433	—	0.42	0.19	2.31	—	2.92
Humptulips	632818	16592	—	0.31	0.26	2.02	0.02	2.61
Humptulips	632819	17309	—	0.46	0.18	2.14	—	2.78
Pooled		**50334**	**—**	**0.40**	**0.21**	**2.16**	**0.01**	**2.77**

[a] Disease prevented tagging.

TABLE 3. Comparison of contribution rates to ocean fisheries of Chehalis and Humptulips Basin wild and hatchery coded wire tagged coho, brood years 1980–83.

Stock	Basin	Estimated ocean recoveries (%)				
		Brood Year				
		1980	1981	1982	1983	Average
Wild	Chehalis	1.80	1.14	0.44	1.11	
	Humptulips	3.59	2.13	0.80	2.69	
Survival ratio (%)[a]		50.14	53.52	55.00	41.26	49.98
Hatchery	Chehalis	0.70	1.25	0.50	1.10	
	Humptulips	1.91	—[b]	0.49	2.77	
Survival ratio (%)[a]		36.65		102.04	39.72	59.47

[a] Chehalis/Humptulips.

[b] Disease prevented tagging.

ment at half the rate of Humptulips River coho. Moreover, that Chehalis River wild coho also survive at significantly inferior rates to Humptulips wild coho constitutes new information. This finding also refutes the alternative explanation for the differential survival between fish from the two river systems proposed by Deschamps and Senn (1969) that SH produces poor quality fish.

Inferior quality of fish released from SH has long been advanced by some to explain their poor performance, particularly in recent years in relation to that of coho released at HH. Clearly, there were differences in "quality" of fish released between the two hatcheries. Results indicate, however, that SH fish were probably superior in quality to those of HH at least in two of the four years. HH's 1981 brood was in such poor condition due to disease that it could not be tagged. (SH fish of this brood were tagged and survived at the highest rate measured thus far (Table 6)). Superior quality of 1982 brood SH fish may also account for their contribution equivalent to that of HH fish, a result inconsistent with comparison of the contribution rates of Chehalis and Humptulips Rivers wild tag groups of this brood. Thus, wildstock evaluations, while certainly more difficult and expensive to conduct, may provide a more reliable measure of subsequent environmental impacts on stocks than comparing performance of tagged hatchery production because of differences inherent between hatcheries and annual variations in fish quality.

An additional indication that Chehalis River stocks experience poor survival is provided by the results of the tagged coho outplanted into the Chehalis River. Some reduction in survival of these groups due to transport and earlier time of release was expected. I esti-

TABLE 4. Estimated contribution rates to ocean fisheries and Grays Harbor gillnet fisheries of tagged hatchery coho smolts released at Simpson Hatchery (on-station) and outplanted (off-station) into tributaries of the Chehalis River, brood years 1980–83.

On/ Off	Brood year	Release date	Tag code	No. tags	Contribution		
					Ocean	Harbor	Total
Off	1980	3/31–4/26	632403	51883	0.15	0.02	0.17
Off	1980	4/2–4/6	632455	53934	0.07	0.02	0.09
On	1980	5/20	632408	52465	0.70	0.14	0.84
Off	1981	4/11–4/14	632648	51230	0.30	0.11	0.41
Off	1981	3/10–3/15	632736	51945	0.11	0.02	0.13
On	1981	4/30–5/9	632647	47734	1.25	0.16	1.41
Off	1982	3/26–3/29	632862	50231	0.03	—	0.03
Off	1982	3–22	632743	48935	0.14	0.03	0.24
On	1982	5–2	632861	45404	0.50	0.28	0.78
Off	1983	3–29	—[a]	50856	0.41	0.40	0.81
Off	1983	3–27	—[b]	49021	0.10	0.14	0.24
Off	1983	4–3	—[c]	50796	0.07	0.03	0.10
On	1983	5–13	—[d]	51319	1.10	0.63	1.73

[a] Two replicate groups; 633032 and 633033.

[b] Three replicate groups; 632829, 632830 and 632831.

[c] Three replicate groups; 632820, 632821 and 632822.

[d] Two replicate groups; 633345 and 633346.

Contribution estimates are based on replicates pooled.

TABLE 5. Estimated contribution rates to ocean fisheries of replicated coded wire tagged coho from a 1983 brood transfer experiment involving release of Humptulips Hatchery stock into lower Chehalis River tributaries, a transfer control group and an overall control group. Both control groups were released into the Humptulips River.

Treatment	Tag code	Number tagged	Estimated ocean recoveries (%)					
			CA	OR	WA	B.C.	AK	Total
Control;	632823	16210	—	0.24	0.06	1.36	—	1.66
released	632824	16564	—	0.36	0.05	2.05	—	2.46
at hatchery	632825	16967	—	0.24	0.10	1.57	0.01	1.92
	Pooled	49741		0.28	0.07	1.66	—	2.01
Transported	632826	17252	—	0.12	0.16	1.07	0.03	1.38
1.5 hours;	632827	17094	—	0.29	0.08	1.45	—	1.82
released	632828	16530	—	0.12	0.15	1.07	—	1.34
at hatchery	Pooled	50876	—	0.18	0.13	1.20	0.01	1.51
Offstation	632820	16742	—	0.02	0.01	0.10	—	0.13
release into	632821	17469	—	—	—	0.05	—	0.05
Chehalis	632822	16585	—	—	—	0.03	—	0.03
River tribs.	Pooled	50796	—	0.01	—	0.06	—	0.07

mated the combined effects of these two variables at approximately 45.5 % by comparing contribution rates of 1983 brood coho released from HH at different times in conjunction with results of the transport study (HH production released May 15 and the transport study groups released April 3 (Tables 2 and 5, respectively)). The substantially lower than expected contribution rates of the outplants relative to releases at SH is further evidence that emigration through inner Grays Harbor is inimical to survival.

Comparison of the contribution rate of the outplanted group from the 1983 brood transfer experiment (0.10 %) to those of the other 1983 brood outplanted groups (0.81 % and 0.24 %) (Table 4) provides more evidence that the survival problem is not related to stock or migration distance from the estuary. The former group was released in tributaries to the lower Chehalis River while the latter two groups were released into the upper Chehalis. These results also tend to counter one local theory; that predation by squawfish (*Ptychocheilus oregonensis*) and or birds in the mainstem Chehalis River is responsible for the low survival.

TABLE 6. Survival from smolt to adult recruitment of Bingham Creek wild and Simpson Hatchery coho based on coded wire tag contribution rates to harvest and escapement, brood years 1980–83.

Brood Year	Tag code	Fishery contribution Ocean	Fishery contribution Harbor[a]	Escapement	Total survival (%)
		Bingham Creek			
1980	632358	1.21	0.26	2.29	3.76
1981	632726	0.87	1.07	5.91	7.85
1982	633027	0.35	0.17	0.50	1.02
1983	633035	0.81	0.97	3.50	5.28
1984	634131	—[b]	—[b]	1.30	—[b]
average		0.81	0.62	3.05	4.48
		Simpson Hatchery			
1980	632408	0.70	0.14	0.41	1.25
1981	632647	1.25	0.16	3.08	4.49
1982	632861	0.50	0.28	0.45	1.23
1983	—[c]	1.10	0.63	1.08	2.81
average		0.89	0.30	1.26	2.45

[a] Includes river sport fishery.

[b] Not available.

[c] Two replicate groups; 633345 and 633346.

If this were true, the groups released into the upper river should survive at lower rates, having been exposed to more predation. (Due to extremely low survival, releases of outplanted coho smolts into the Chehalis River system were discontinued after the 1983 brood.)

Results of the extensive smolt trapping employed in this evaluation demonstrate that the Chehalis River system's freshwater production potential is commensurate with other systems under study throughout the state (Seiler et al. 1984). Potential production levels, however, are rarely achieved in the Chehalis River due to underescapement. To help mitigate this chronic condition, WDF has outplanted up to 2 million coho smolts and up to 5 million coho fry into the Chehalis River system each year. These outplanting programs were initiated after production studies in 1976 and 1977 estimated upper Chehalis River coho smolt production at only 116 000 and 50 000, respectively (Brix and Seiler 1977 and 1978). They estimated potential smolt production at over 1.8 million smolts from this 2383 km^2 portion (42 %) of the Chehalis River Basin and attributed the low actual production to underescapement.

In comparison, I estimated that 1984 brood coho smolt production (trapping year 1986) for the same portion of the watershed was nearly 900 000 smolts. My methods and those of Brix and Seiler were nearly the same. This production resulted from a very large spawning escapement. Coho escapement to the entire Grays Harbor Basin was estimated at over 100 000 in 1984. This resulted from unanticipated high marine survival and restrictive harvest controls, consequently, most of the run escaped. One precise measure of this is provided by the 1981 brood Bingham Creek wild stock which was tagged in 1983 and returned as adults in 1984. Total survival from smolts to adult recruitment for this stock measured nearly 8 %, the highest we have recorded; 75 % of the fish that survived, escaped fisheries to return in 1984 (Table 6).

TABLE 7. Summary of coho spawning escapement and smolt production measured upstream and downstream, respectively, at the Bingham Creek trapping station, brood years 1980–87.

Brood year	Spawning escapement Males	Spawning escapement Females	Smolt production	Smolts/ female
1980	366	355	31 806	89.6
1981	1 070	1 268	33 464	26.4
1982	917	946	43 945	46.5
1983	699	543	30 939	57.0
1984	3 740	2 869	25 205	8.8
1985	1 010	914	22 233	24.3
1986	1 410	1 445		
average			31 265	48.8[a]

[a] Does not include brood year 1984 due to large escapement.

Although smolt production was measured in 1986 at the point in the mainstem Chehalis River where 42 % of the total basin's area lies upstream, the production measured is probably less than this proportion of the entire Chehalis Basin's 1984 brood coho smolt production. This expectation is based on a qualitative assessment of the entire Chehalis River system's stream habitat that found a higher proportion of poor habitat in the upper basin than in the lower basin (downstream of the scoop trap site) (Phinney and Bucknell 1975). Further, the level of production measured in 1986 is probably an underestimate of the upper basin's potential to produce coho smolts because of the negative impact on rearing coho from the dry summer of 1985 (Smoker 1955; WDF and NWIFC 1987). As a measure of this effect, in 1986, smolt production at Bingham Creek was only 72 % of the previous four year average smolt production (Table 7). Given sufficient escapement then, and average environmental conditions during freshwater residence, the coho smolt production potential of the upper Chehalis River system would exceed 1 million. Extrapolation of this production level to the watershed area downstream of the scoop trap and accounting for the relatively higher habitat quality in the lower basin, the total coho smolt production potential of the Chehalis River system is estimated at two to three million.

Not only has the Chehalis River's capacity to produce coho smolts been empirically verified by this investigation, but the ongoing production studies at the Bingham Creek station also have found the production per spawner to be equivalent to rates measured elsewhere in the state (Seiler et al. 1984). At an average production rate of 50 smolts per female, an average survival to escapement rate of 4% is required to return two adults to spawn at the replacement level. Survival to return of the Bingham Creek wildstock has been well below this rate in three of the last five seasons (Table 6). Bingham Creek has received adequate escapement each year only because of its proximity to SH which annually releases 1 to 2 million coho smolts (hatchery returns contribute to the spawning escapement).

These low return rates demonstrate how poor survival results in underescapement, a condition which further depresses production. Even severe restrictions on harvest have not insured adequate escapements. The total survival (catch plus escapement) of wild coho in the Chehalis, as indicated by the tagged Bingham Creek coho, has been below the critical four percent level in three of the last five years (Table 6). Not only has the low survival devastated the health of Chehalis River coho stocks, but fishermen, particularly harbor gillnetters and river sportsmen have foregone considerable harvest opportunities as a consequence.

As the largest watershed in the state, outside the Columbia River, the Chehalis Basin's substantial anadromous fish production potential provides strong incentive to identify and if possible, solve the survival problem affecting Chehalis Basin stocks. The following illustrates the annual estimated cost of the poor survival in coho alone.

Stock	Smolt production		Differential mortality		Marine survival		Estimated no. adults lost
Hatchery	2 million	×	50%	×	5%	=	50 000
Wild	2 million	×	50%	×	9%	=	90 000
Total							140 000

This lost harvest represents an annual cost of one to two million dollars per year or more using conservative values of $10 to $20 per fish. Addition of the values of the foregone chinook and steelhead harvests may double this annual cost.

Resolution Efforts

Water quality and its impact on aquatic resources is a major concern in Washington State. Consequently, the survival problem documented herein has generated considerable interest and some controversy. As a result, a cooperative effort comprised of industry, federal, state and local government agencies, academic and other interest groups has been formed to address the issues involved. Within this group, consensus has been reached that a significant survival problem affects Chehalis Basin anadromous fish stocks. Agreement on the causative factor(s), however, has not been reached.

In an effort to determine the cause(s) of this poor survival, WDF requested and obtained the assistance of federal and university fisheries scientists to design a study plan. This plan simultaneously evaluates four hypothesis that have been developed to explain the poor survival of salmonids following emigration from the Chehalis River. These hypotheses are as follows:

1) The Chehalis River produces smolts that have an impaired ability to adjust to seawater (i.e. smoltification).
2) Pathogens present in the Chehalis system induce delayed mortalities, possibly by preventing successful smoltification.
3) The water quality of the lower Chehalis River and inner Grays Harbor induces chronic physiological stresses which prevent successful smoltification, reduce the competancy of the immune system to such an extent that the fish succumb to disease and or become more susceptible to predation.
4) Populations of natural predators (birds and squawfish) in the Chehalis River are great enough to account for some or all of the poor survival.

The study, which will be conducted in 1988 and 1989, is comprised of three major parts. One evaluates predator impacts, another addresses the smoltification status, health and stress levels of coho juveniles in freshwater and in the estuary, while the third examines, via bioassay protocols, the effects of pulp mill and sewage treatment effluent and Chehalis River water on smolting coho salmon. The overall approach of the study is to compare various parameters measured on Chehalis River coho against those of Humptulips River coho which serve as a natural control. Funding for this investigation has been provided by a $400,000 appropriation from the state legislature. The U.S. Environmental Protection Agency and the WDOE have developed and will conduct a detailed water quality assessment integrated to the survival study.

As these investigations are presently underway, forthcoming results will provide the basis for further discussion concerning the impact of Grays Harbor water quality on Chehalis River anadromous salmonid stocks. The Grays Harbor case history, however, has important generic implications to solution of water quality related fish survival problems. First, the scientific burden of proof is extremely large when attempting to establish links between water quality and its impacts on fish stocks. The socioeconomic inertia created by fears of costly water pollution controls is great and, as this case demonstrates, an overwhelming body of empirical evidence is required to instigate "decisive action". For Grays Harbor, "decisive action" entails continued study including low-likelihood hypotheses as a means to build government and industry consensus.

Costs of overcoming the socioeconomic inertia and consensus building, although rarely quantified, can be substantial. In the case of Grays Harbor, calculable costs include the many years of resource monitoring and research efforts (sometimes repetitive) in addition to the many year's accumulation of lost harvest benefits. Potentially even more serious, and certainly more difficult to estimate, however, are the long term risks to the productive potential of the resource by altering stock composition and character and by devaluing the benefits of harvest and other habitat protection programs. As an example, because of recent low harvests in Grays Harbor there is considerable support to remove the "constraint" of wild salmon escapement goals and implement large scale hatchery programs.

The importance of directly measuring, at the stock level, and with sufficient precision, the health and status of fishery resources is also clear with respect to evaluating and monitoring long-term status of water quality. In Grays Harbor, regulated improvements in water quality via discharge permits and waste water treatment criteria were assumed to translate into improved fish survival. National environmental law requires continued improvements in waste water management (reductions in volumes and toxicity). As an example, effluent from one of the pulp mills (over 90×10^6 L d^{-1}) that is presently discharged at a pH of 3 or less will, in 1990 or 1991, require neutralization before release to the harbor. Effects of incremental improvements or changes in effluents on fish stocks will remain difficult or impossible to predict. Aquatic scientists should question the utility of laboratory toxicity tests on effluents as a means to protect aquatic resources. Direct biological monitoring represents the only means to verify whether regulatory measures are sufficient to provide a healthy environment for fish life. To this end, continued monitoring of Chehalis River coho survival is planned.

Acknowledgements

The contributions numerous individuals within the Washington Department of Fisheries' Engineering, Salmon Culture, Habitat Management, Harvest Management and Research Divisions have made to this study are appreciated. Special thanks are due Rich Lincoln for his steadfast support and direction. Sam Wright was instrumental in establishing the coastal evaluation station. Pat Hanratty and Steve Neuhauser supervised the crews of technicians who performed the demanding work of wild salmon trapping and tagging. Lee Blankenship was responsible for some of the early wildstock tagging and all of the hatchery tagging. I.K. Birtwell and C.D. McAllister reviewed an early manuscript. Kurt Fresh also reviewed this paper and provided helpful comments. Funding for these studies was provided by the U.S. Fish and Wildlife Service, the National Marine Fisheries Service and the State of Washington.

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Protecting Fraser River Salmon (*Oncorhynchus* spp.) From Wastewaters: An Assessment

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Abstract

SERVIZI, J. A. 1989. Protecting Fraser River salmon (*Oncorhynchus* spp.) from wastewaters: an assessment, p. 136–153. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

The daily volume of wastewater discharged to the Fraser River system has increased 3-fold since 1965. For the Upper Fraser and Thompson River systems the increases were 38 and 12 times, respectively, due mainly to addition of five bleached kraft pulp mills and a thermomechanical/chemi-thermomechanical pulp mill. Industrial and municipal wastewaters were required to meet toxicity criteria specified by regulatory bodies. Compliance was approximately 77% on a volume basis. Data for Pacific salmon populations were reviewed to determine whether these stocks were adequately protected from wastewaters. Stocks of sockeye (*Oncorhynchus nerka*) and pink (*O. gorbuscha*) salmon increased. There was no indication that treated wastewater precluded successful migration and spawning of these two species. Data for chum (*O. keta*), coho (*O. kisutch*) and chinook (*O. tshawytscha*) were not adequate to differentiate potential effects of wastewaters on stocks from the effects of other habitat impacts, natural variability and management practices. There were indications that coho were at risk owing to wastewaters in some urban streams. There was potential for impact on juvenile chinook salmon which overwinter in the Fraser River, especially in or near dilution zones.

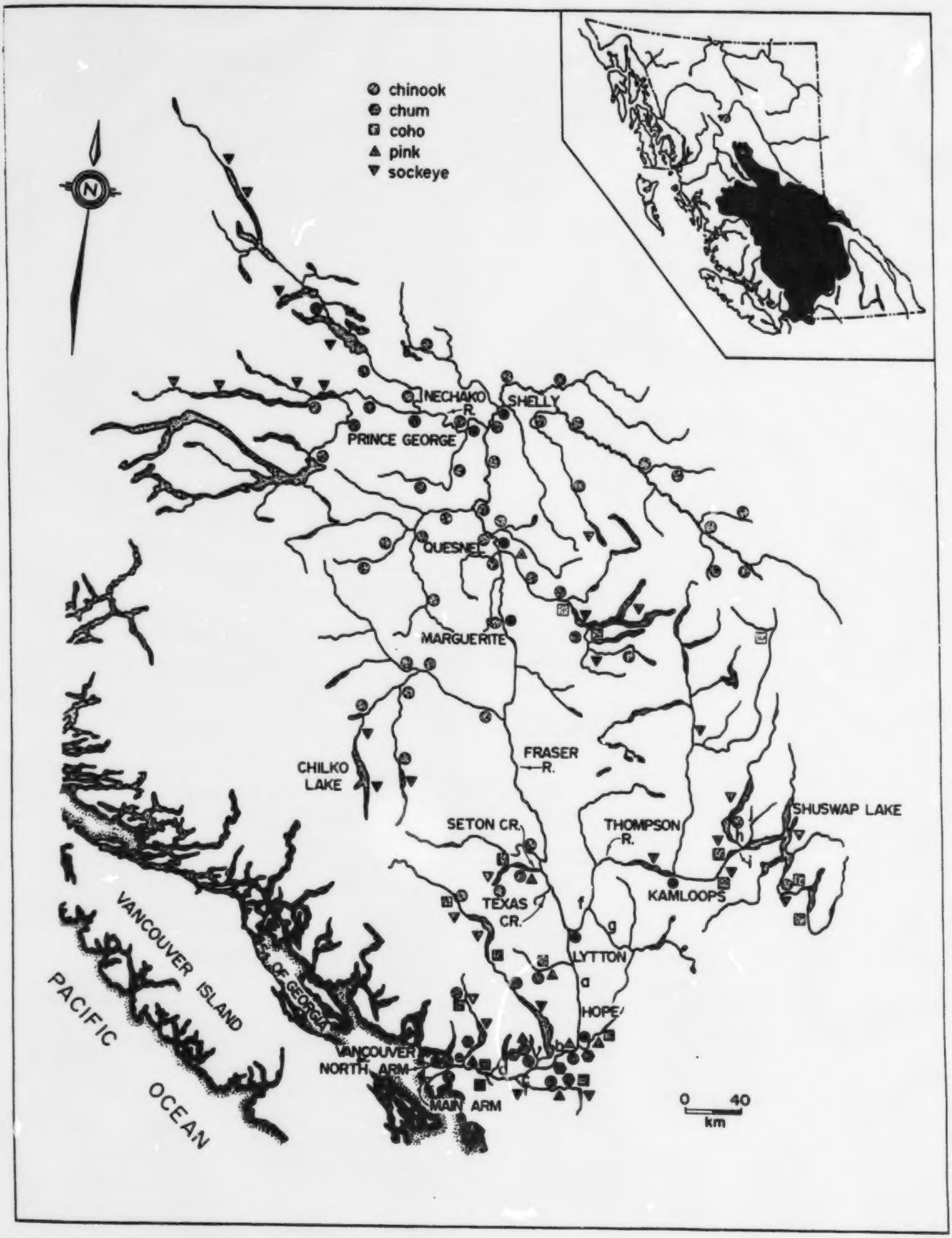
Résumé

SERVIZI, J. A. 1989. Protecting Fraser River salmon (*Oncorhynchus* spp.) from wastewaters: an assessment, p. 136–153. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Le volume quotidien d'eaux usées rejetées dans la réseau du fleuve Fraser a triplé depuis 1965. Dans les réseaux de la partie supérieure du fleuve Fraser et de la rivière Thompson, ce volume a augmenté respectivement de 38 et 12 fois par rapport à cette époque, phénomène dû principalement à la construction de cinq usines de pâte kraft blanchie et d'une usine de pâte utilisant un procédé thermomécanique/chimico-thermomécanique. Les eaux usées industrielles et municipales doivent respecter les critères de toxicité fixés par des organismes de réglementation. Le pourcentage de conformité était d'environ 77% en fonction du volume. On a examiné les données concernant les populations de saumons du Pacifique afin de déterminer si ces stocks étaient protégés de façon adéquate contre les produits chimiques des effluents. Les stocks de saumons rouges (*Oncorhynchus nerka*) et roses (*O. gorbuscha*) ont augmenté. Rien n'indiquait que les eaux usées traitées pouvaient entraver la migration et la fraie de ces deux espèces. Les données relatives aux kétas (*O. keta*), cohos (*O. kisutch*) et quinnats (*O. tshawytscha*) n'étaient pas suffisamment complètes pour établir une distinction entre, d'une part, les effets possibles des eaux usées sur les stocks et, d'autre part, les répercussions d'autres sources sur les habitats et les incidences de la variabilité naturelle et des techniques de gestion. Certains signes permettaient de croire que les saumons cohos étaient en péril à cause du rejet des eaux usées dans certains cours d'eau à proximité des villes. Il y avait des risques d'effets préjudiciables sur les saumons quinnats juvéniles qui passent l'hiver dans le fleuve Fraser, particulièrement dans les zones de dilution ou à proximité de celles-ci.

Introduction

The Fraser River is 1368 km long and drains a watershed (230 400 km ^{2}) composed of mountains, interior plateaus and coastal valleys (Fig. 1). Downstream of Port Mann, Fraser River flow divides into the North Arm (15%) and the Main Arm (85%). Climate over most of the watershed is continental but the south-


chinook
chum
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pink
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N
NECHAKO R.
SHELLY
PRINCE GEORGE
QUESNEL
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CHILKO LAKE
SETON CR.
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KAMLOOPS
SHUSWAP LAKE
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LYTTON
a
HOPE
b
c
d
e
VANCOUVER
NORTH ARM
MAIN ARM
VANCOUVER ISLAND
ST. OF GEORGIA
PACIFIC OCEAN
0 40
km

FIG. 1. Fraser River watershed and distribution of Pacific salmon spawning and rearing: (a) Hell's Gate; (b) Agassiz; (c) Chilliwack; (d) Mission; (e) Port Mann; (f) Spences Bridge; (g) Nicola River; (h) Adams River; (i) Little River; (j) Scotch Creek. Symbols indicate spawning/rearing.

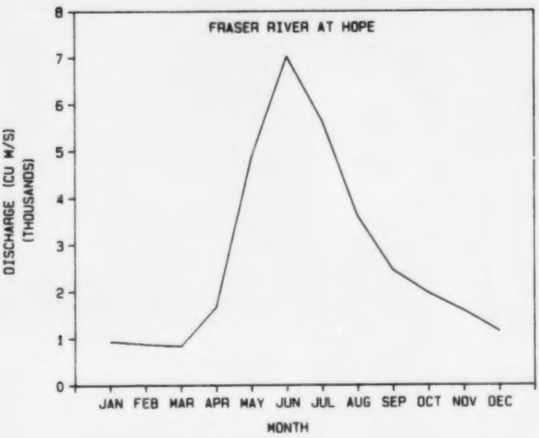

FIG. 2. Mean monthly discharge in the Fraser River at Hope (1912–84).

westerly portion is coastal. Flows in the Fraser River are characterized by a winter minimum and a late spring maximum associated with runoff from snowmelt (Anon. 1985) (Fig. 2). The 10-yr, 7-day average low flows (m^3 d^{-1}) at gauging stations along the Fraser River are; Shelley (9.86×10^6), Marguerite (21.3×10^6), Texas Creek (31.8×10^6), Hope (38.7×10^6) and Mission (69.7×10^6). In the Thompson River at Spences Bridge the 10-yr, 7-day average low flow was 11.3×10^6 m^3 d^{-1} (Anon. 1986a).

The Fraser River and its tributaries support five species of Pacific salmon (*Oncorhynchus* sp.) with an estimated annual average wholesale value of $100 million over the past decade (P. Kopas, Department of Fisheries and Oceans, Vancouver, B.C., V6E 2P1, pers. comm.). More than 270 streams, rivers and lakes are used for migration, spawning and rearing. The Fraser supports an average annual stock of nearly 14 million adult Pacific salmon making it one of the world's major salmon producers (Northcote and Larkin 1989). Annual stock sizes vary widely about the average owing to cyclic dominance among sockeye (*O. nerka*) and pink (*O. gorbuscha*) on odd-numbered years. It has been estimated that the average can be increased to 25 million or more through management and enhancement (Anon. 1986b).

Except near the river mouth, there was little industrialization or population on the Fraser River watershed in 1960. In recognition of the potential for industrial and population growth and the need to protect Fraser River salmon from wastewaters, the Department of Fisheries, assisted by the International Pacific Salmon Fisheries Commission, adopted a strategy in the period 1950–60 calling for treatment to detoxify effluents before discharge. This strategy was based on several factors: (1) an awareness of decline in aquatic resources in other major industrialized rivers worldwide; (2) recognition of inadequate knowledge of (a) the effects on salmon of effluents acting singly or in combination; and (b) the behavior of salmon, especially juveniles, throughout the Fraser system; (3) the belief that pollution control measures should be taken in advance of measurable impact; and (4) dilution in receiving waters should serve as a safety factor and not as the first line of defense against pollutants. This report reviews application of this strategy and examines whether the objective of protecting salmon has been achieved. In so doing, the report presents a perspective on an observation by Hamilton (1976), ''Reduction of discharges or the toxicity of discharges is laudable but the idea that these regulations are significantly protecting the environment has not been generally substantiated to my knowledge''.

Effluent Criteria

The first major application of the ''treatment before discharge'' strategy occurred with the advent of proposals around 1960 to construct bleached kraft pulp mills in the interior of the watershed (Anon. 1961). Research was undertaken before construction to develop detoxification criteria for these effluents using sockeye and pink salmon at various freshwater life stages, including egg to fry (Servizi et al. 1966). Using the knowledge available and Section 33 of the Fisheries Act, Environment Canada formulated The Pulp and Paper Regulations and Guidelines requiring 80% survival of rainbow trout (*Salmo gairdneri*) in 65% effluent during a 96-h continuous flow bioassay (Environ. Can. 1971, 1972). In addition, the B.C. Pollution Control Board issued Objectives in 1971, subsequently revised in 1977, specifying effluent criteria for pulping processes, including limits on toxicity (Table 1). Thereafter, toxicity criteria were included in Objectives for all municipal and industrial sectors except food processing, agricultural and miscellaneous industries (Table 1). Objectives were included in the effluent discharge permits issued by the Waste Management Branch (B.C. Ministry of Environment and Parks).

For industrial and municipal wastewaters, the Pollution Control Board specified graduated objectives. Level A Objectives are described as the desirable goals for all discharges and generally apply to all new discharges and to existing installations where discharges are altered significantly in quantity or quality. Levels B and C were considered interim and initial levels, respectively, achievable by then current pollution control and wastewater treatment techniques. Federal Guidelines and Regulations specified effluent criteria achievable by best practicable technology. *The Fisheries Act* would also be applied to control discharges where stricter criteria might be required.

TABLE 1. Toxicity criteria of British Columbia pollution control objectives.

Source of wastewater	Effluent toxicity objectives (96-h LC50, % v/v) Level A	B	C	Effective date and reference
Pulping Processes	100	30	—	Poll. Cont. Bd. 1977[c]
	90	90	17	Poll. Cont. Bd. 1971
Municipal[a]	100[b]	75[b]	—	Poll. Cont. Bd. 1975
Mining, Smelting and Related Industries	100	80	—	Poll. Cont. Bd. 1979[c]
	100	80	20	Poll. Cont. Bd. 1973
Petroleum Refineries	100	75	5	Poll. Cont. Bd. 1974
Chemical Industry	100	90	50	Poll. Cont. Bd. 1974
Food Processing, Agricultural and Miscellaneous Industries	none specified			Poll. Cont. Bd. 1975

[a] Levels designated as AA and BB.

[b] Prior to disinfection by chlorination.

[c] Revised.

TABLE 2. Daily volumes of municipal and industrial wastewaters discharged to the Fraser River system.[a]

	1965 $m^3\ d^{-1}$	1985 $m^3\ d^{-1}$
Municipal		
Thompson R.	19 500	28 600
Fraser R.; Upstream of Lytton	13 100	111 700
Fraser R.; Lytton to Port Mann	10 000	50 000
Fraser R.; Downstream of Port Mann	170 000	326 000
Fraser R.; Landfill leachate	b	6 000
Industrial		
Thompson R.	nil[c]	199 500
Fraser R.; Upstream of Lytton	1 400	444 400
Fraser R.; Lytton to Port Mann	nil	nil
Fraser R.; Downstream of Port Mann	290 000	360 000
Total Wastewater at River Mouth	504 000[d]	1 526 200

[a] Compiled from Swain and Holms (1985a, b), Swain (1980), Anon. (1984), files of British Columbia Waste Management Branch, at Prince George, Williams Lake, Kamloops and Victoria and B.F. Talbot, Greater Vancouver Regional District, Burnaby B.C., V5H 4G8 (pers. comm.).

[b] No record.

[c] Increased to 43 300 in December 1965.

[d] Increased to 547 300 in December 1965.

The toxicity of municipal effluents was measured prior to disinfection by chlorination (Table 1). However, in recognition of the high toxicity of residual chlorine in municipal effluents and tests which demonstrated the feasibility of its removal (Martens and Servizi 1975), dechlorination was adopted at Lulu Island (1974) and Annacis Island (1975) sewage treatment plants (STP) by the Greater Vancouver Sewerage and Drainage District. Subsequently, through provisions of the *B.C. Pollution Control Act*, dechlorination was applied at some smaller STP's on the Fraser River watershed.

Wastewater Input

The major inputs of wastewater of the Fraser River systems occur in the upper Fraser River at Prince George and Quesnel, at Kamloops on the Thompson River and in the Lower Fraser River from Port Mann to the mouth. Wastewaters are summed throughout the river length since many toxic contaminants, especially chlorinated phenolics, are only slowly degraded and persist in the river in spite of treatment (Voss and Yunker 1983; Voss 1984; Leuenberger et al. 1985).

Prior to 1965, the Fraser River upstream of Lytton plus the Thompson River, received about 32 600 m^3 d^{-1} of municipal sewage (Table 2) and 1400 m^3 d^{-1} of industrial effluent. The first major industrial discharge (43 300 m^3 d^{-1} commenced in late 1965 with start-up of a bleached kraft pulp mill (Kamloops Pulp and Paper Ltd.) on the Thompson River at Kamloops. In 1966, Prince George Pulp and Paper Ltd. and Northwood Pulp and Paper Ltd. commenced operation of two bleached kraft pulp mills located 2.4 and 12 km, respectively, upstream of the confluence of the Fraser and Nechako Rivers at Prince George. These two mills added about 179 000 m^3 d^{-1} of effluent to the Fraser River. The fourth bleached kraft pulp mill (Intercontinental Pulp and Paper Co. Ltd.) commenced operation in 1968 at Prince George and added 124 000 m^3 d^{-1} of effluent to the Fraser River about 1 km upstream of the Nechako River confluence. All four mills employed biological treatment of effluents at the outset of their operations with varying degrees of success. The five-day aerated lagoon at Kamloops Pulp and Paper proved more stable than the 24-hour treatment systems at the other three mills. To meet Federal Regulations and Provincial Objectives, the effluent treatment system at Northwood Pulp and Paper was upgraded to a 5-day retention aerated lagoon in late 1974. For similar reasons, Prince George Pulp and Paper and Intercontinental Pulp and Paper converted to adjoint 4.5-day retention aerated lagoon in 1978.

Kamloops Pulp and Paper became Weyerhaeuser Canada Ltd. and expanded design production approximately 5-fold in 1972. Effluent flow increased to about 182 000 m^3 d^{-1} and the aerated lagoon was expanded to maintain 5 days treatment. Cariboo Pulp and Paper commenced operation of a bleached kraft pulp mill at Quesnel in 1972, adding about 87 000 m^3 of treated effluent to the Fraser River.

Quesnel River Pulp Co. commenced operation of a thermomechanical pulp mill at Quesnel in late 1981. Chemi-thermomechanical pulp production was added

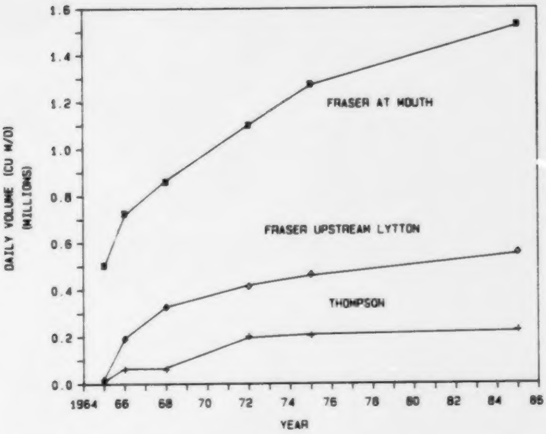

FIG. 3. Daily wastewater discharges to the Fraser River system.

in 1983. An effluent flow of 7200 $m^3 d^{-1}$ was treated in an aerated lagoon before discharge to the Fraser River, but the treatment system proved to be underdesigned. A treatability study demonstrated that major modifications would be required to upgrade effluent treatment (Servizi and Gordon 1986). The company proposed a second treatability study in 1986 to examine alternatives.

In 1982 Northwood Pulp and Paper commissioned a second bleached kraft mill to double production. Effluent flow increased to about 144 000 $m^3 d^{-1}$ but aerated lagoon capacity was increased to give a treatment time of about 8 days.

By 1985, the amount of treated industrial and municipal effluent entering the Fraser River system upstream of Lytton totalled 556 100 $m^3 d^{-1}$, an increase of approximately 38 times since 1965 (Fig. 3). For the Thompson River, treated wastewater discharges increased just under 12-fold to 228 100 $m^3 d^{-1}$ between 1965 to 1985. Approximately 79 % of the wastewater discharged upstream of Lytton was secondary-treated pulp mill effluent.

From Lytton downstream, up to 180 000 $m^3 d^{-1}$ of municipal sewage was being discharged to the Fraser River without treatment in 1965 (Table 2). The amount of industrial effluent was approximately 290 000 $m^3 d^{-1}$, plus an additional 40 000 $m^3 d^{-1}$ of uncontaminated cooling water. Little of the industrial effluent was treated before discharge because Pollution Control Objectives had yet to be developed. The Lulu Island and Annacis Island sewage treatment plants (STP) began operating in 1973 and 1975, respectively, applying primary treatment, chlorination and dechlorination to municipal sewage containing an industrial wastewater component (Cain and Swain 1980). These STP's discharge to the Main Arm of the Fraser River at 5 and 23 km from the mouth, respectively. Secondary treatment was applied to various small municipal discharges during the 1970's. By 1985, the annual average municipal sewage discharge to the Fraser River downstream of Lytton was 376 000 $m^3 d^{-1}$ of which 87 % was primary treated and dechlorinated and the remainder received secondary treatment. The industrial discharge, totalling approximately 360 000 $m^3 d^{-1}$, was required to meet Pollution Control Objectives for each industry. Landfill leachates contributed about 6000 $m^3 d^{-1}$.

The sum of wastewaters discharged to the Fraser River system upstream of its mouth increased from 504 000 $m^3 d^{-1}$ in 1965 to 1 526 000 $m^3 d^{-1}$ by 1985 (Fig. 3). Most of the increase occurred by 1975. Forty-one percent of the total wastewater in 1985 was secondary treated effluent from six pulp mills in the upper watershed and a further 20 % was primary treated, dechlorinated municipal sewage discharged by the Annacis Island sewage treatment plant.

At 10-yr, 7-day average low river flows, the calculated concentrations for wastewater flows in 1985 ranged from 3.4 % near Prince George to 1.9 % near Hope, when fully mixed in the river (Table 3). In dilution zones, before effluents are fully mixed with the river, concentrations would be much higher. For example, at Annacis Island STP, calculations based on field measurements predicted effluent concentrations of 20–25 % above the diffusers at 1986 effluent flow volumes owing to multiple dosing associated with tidal changes (Singleton 1980). Concentrations decreased to about 0.6 % and less at the edge of the dilution zone. Accuracy of these predictions has not been confirmed. The total of slack tides per month range from more than 50 h in January to about 30 h in May. The maximum duration of slack tide was 5.3 h (Narayanan 1980). Effluent concentrations in the vicinity of pulp mills at Prince George and Quesnel in October were in the range 3.6–2 % at 50–90 m downstream of diffusers

TABLE 3. Wastewater concentrations for 1985 effluent volumes and 10-yr, 7-day average low river flows.[a]

	10-Year, 7-Day Low Flow $m^3 d^{-1} \times 10^3$	Wastewater 1985 $m^3 d^{-1} \times 10^3$	Wastewater Conc %
Thompson R. near Spences Br.	11 256	228	2.0
Fraser R. upstrm of Pr. George	9 861	340	3.4
Fraser R. dwnstrm of Quesnel	21 288	501	2.4
Fraser R. near Hope	38 663	733	1.9
Fraser R. near mouth	78 103	1 526	2.2

[a] Assuming complete dispersion of wastewater in the river flow.

[b] Based on river flow at Port Mann equal to 1.12 times flow at Mission. (Anon. 1985).

based on calculations using sodium as a tracer (G. Derksen, Environmental Protection, West Vancouver, B.C., V7T 1A2, pers. comm.). At 1000 m, effluent concentrations were in the range 0.5–1.4 %.

Effluent Monitoring

Under terms of provincial Discharge Permits, permittees are required to monitor effluent quantity and quality. Selected physical and chemical characteristics are specified according to the type of effluent. Since potential impact on aquatic life may be caused by a mixture of contaminants not readily measured directly, fish bioassays are used as a means of integrating the combined toxic action of residues. Accordingly, for major discharges, effluents were also monitored using bioassays. In the case of pulp mills, Federal Regulations specified 80 % survival in 65 % effluent during a 96-h continuous flow bioassay. Static tests were commonly conducted for reasons of practicality. Being new installations, pulp mills on the Fraser River water shed fell under Level A of the Provincial Objectives. These objectives specified a 96-h LC50 of 90 % v/v in 1971 which was raised to 100 % v/v in 1977 (Table 1).

Effluents from the pulp mill at Kamloops failed only occasionally to meet Federal and Provincial criteria for toxicity. However, at Northwood Pulp and Paper prior to 1974, and at Prince George Pulp and Paper and Intercontinental Pulp prior to 1978, approximately 70, 18 and 50 %, respectively, of samples met Federal Regulations because 24-h retention aerated treatment systems were incapable of detoxifying effluents consistently. Thereafter, nominal 5-day retention aerated lagoons were installed and effluents were commonly acutely non-lethal.

Calculations using detoxification records for the three pulp mills at Prince George during 1976–77 concluded that, in theory, there was potential for sub-lethal stress conditions in April 1977 downstream of the three mills (Anon. 1984). This conclusion was based on application factors and the assumption that a high combined mean toxicity of effluents occurred simultaneously with 7-day low river flow. A similar review for 1978–82 suggested that sub-lethal stress was extremely remote because detoxification performance improved.

At Cariboo Pulp and Paper the record of compliance with Federal Regulations was 79 % for 1972–74. Compliance decreased to 53 % through 1983, but increased to 81 % thereafter, owing to improvements to the in-plant and out-plant pollution control systems. Treated effluent from Quesnel River Pulp Co. was seldom in compliance owing to an underdesigned and overloaded aerated lagoon treatment system. Wastewaters from Belkin Inc. (11 400 m^3 d^{-1}, paperboard from paper recycling), which are discharged to the North Arm of the Fraser River, frequently failed to meet Level A Objectives for toxicity. On the other hand, wastewaters from Scott Paper Co. Ltd. (14 000 m^3 d^{-1}), which are also discharged to the North Arm, consistently met Level A Objectives.

During a study in 1976, final effluent discharged to the Main Arm from Annacis Island STP consistently failed to meet a 96-h LC50 of 75 % v/v (Level B, Table 1) as specified in the discharge permit (Servizi et al. 1978). Monitoring tests (25) conducted by B.C. Research usually met Level B toxicity criteria (Singleton 1980). The reason for the difference in the two sets of results was not determined. At Lulu Island STP final effluents were more toxic than the 75 % 96-h LC50 specified (Martens and Servizi 1975).

There are numerous much smaller discharges of secondary treated municipal sewage to the Fraser River and tributaries. In some cases these effluents are dechlorinated following disinfection and in the absence of residual chlorine, these would be expected to exhibit little or no acute toxicity (Esvelt et al. 1973) and thus would generally meet Level A Objectives.

Receiving Habitat Monitoring

Upper Fraser River

Since the pulp mills on the Thompson and upper Fraser Rivers discharge large volumes of effluent, the companies are required to monitor the receiving habitat using physical, chemical and biological methods. In addition, some surveys have been conducted by regulatory agencies.

A summary of annual surveys conducted between 1963 and 1981 near Prince George indicated that total residue, dissolved sodium, color and sometimes nutrients were slightly elevated downstream of the three pulp mills when compared to control stations (Anon. 1984). Similar results were obtained in 1984 (Dwernychuk 1985). Based on measured values of Biochemical Oxygen Demand (BOD) and dissolved oxygen, calculations indicated natural dissolved oxygen levels would be little affected by present BOD loadings (Anon. 1984). This finding agrees with an earlier assessment made before pulp mills were in place (Anon. 1961). Total phenols were measured in 1984 and found marginally higher downstream of mill discharges in October but were non-detectable in September. This result may have been related to greater dilution of effluent in September since river flow was 54 % greater than in October. For river benthic invertebrates, there were similarities between communities inhabiting areas immediately downstream of effluent diffusers (Anon. 1984). In addition, there was a significant increase in benthic invertebrate population density downstream of the last operational diffuser. These results were attributed to organic enrichment. There was no indication from the 1984 survey of a negative impact on the benthic community (Dwernychuk 1985). These surveys were not designed to determine whether juvenile salmon inhabited the Fraser River in the vicinity of the discharges.

In October 1980, a chemical survey of effluents, fish and sediments was conducted at Prince George (Rogers and Mahood 1982). About 30 chlorinated phenols, organic acids and neutral compounds were detected in treated pulp mill wastes. Various chlorinated organics common to municipal sewage, including chloroform, were detected in effluent from the secondary municipal sewage treatment plant. Bridgelip suckers (*Catostomus columbianus*) contained organic compounds which may have originated in municipal sewage and pulp mill effluents but neither chlorinated organic compounds nor resin acids were detected in resident fish. Sediments were contaminated with substances derived from pulp mill effluents and from unknown sources.

Chlorinated phenolics of pulp mill origin were detected in the upper Fraser River 50 km downstream of the nearest pulp mill (Voss and Yunker 1983). Throughout the study area, concentrations of chlorinated phenolics were three to five orders of magnitude below acutely lethal levels. Data also demonstrated that pulp mills were not the primary sources of penta- and tetra-chlorophenol in the upper Fraser River. Since these two substances are widely used to preserve lumber at sawmills, it is possible that some enter the Fraser River from these uses. These authors concluded that there were insufficient data on which to assess the long-term effets of chlorinated phenolics on aquatic life in the Fraser River.

Thompson River

Complaints from the public concerning water color, benthic algal growths, tainted fish and declines in steelhead (*Salmon gairdneri*) populations led to studies of the Thompson River in 1973-75 (Anon. 1976). The study concluded that: (1) Color was caused by pulp mill effluent; (2) Pulp mill effluent and municipal sewage, both treated, seriously reduced palatability of salmonids; (3) Reasons for decline in the steelhead population were not determined; and (4) Nuisance growths of benthic algae were attributed to elevated levels of phosphorus. The pulp mill added about 47 % of winter phosphorus loadings, the city of Kamloops contributed 9 % from sewage lagoons and 44 % originated from background sources upstream (Bothwell and Daley 1981). Subsequently, the City of Kamloops reduced phosphorus discharge by partial land disposal of sewage in 1985.

Mountain whitefish (*Prosopium williamsoni*) collected in the Thompson River in March 1982 contained a series of petroleum hydrocarbons plus trace organic compounds typical of municipal sewage (Rogers and Mahood 1983).

Lower Fraser River

Surveys of benthic, epibenthic and drift fauna in the Fraser River between Hope and the mouth in 1972 and 1973 revealed greater benthic biomass and more pollution-tolerant organisms in the North Arm than in the Main Arm (Northcote et al. 1976). Local sources of nutrient enrichment and pollutants were cited as possible causes of this condition, although saline intrusions in the lower reaches of the river may also have influenced the relative abundance of pollution-tolerant organisms. Chapman and Brinkhurst (1981) concluded that seasonal shifts in benthic infaunal species were correlated with seasonal variation of interstitial sediment salinities.

Studies of water quality and aquatic biota in the Fraser River estuary indicated most water quality characteristics were not measurably changed by major discharges, except in dilution zones and backwaters (Anon. 1979). In the dilution zone at Annacis Island STP, multiple dosing could create conditions unsafe for fish at minimum river flows (Singleton 1980). In some backwaters, dissolved oxygen decreased to a point which could endanger aquatic life (Stancil 1980). Some accumulation of heavy metals and organic contaminants was noted in aquatic biota. The amounts of contaminants detected in fish were low compared to standards for human consumption (Garrett 1980; Stancil 1980). Later surveys included sockeye salmon returning from the ocean and in these surveys metals were within standards for human consumption (Singleton 1983).

A survey of water in the North Arm of the Fraser detected analytically significant levels of 2,3,4,6-tetra chlorophenol (TeCP) and pentachlorophenol (PCP) (Jacob and Hall 1985). Continuous monitoring revealed peaks of TeCP and PCP which would not have been detected in grab samples. Leeches (*Hirudinea marmorata*) were found to bioconcentrate TeCP and PCP when exposed for seven days to Fraser River water. Chlorophenols were 100 to 1400 times greater in fish, (no salmonids), than in waters of the North Arm in 1984 (Carey et al. 1986). Singleton (1983) reported chlorophenols in largescale suckers (*Catostomus catostomus*) collected in the Fraser River near Chilliwack and in the North and Main Arms. However, the toxicological implications of the levels measured were not known. Swain (1986) found chlorophenols and polychlorinated biphenyls higher in sediments from the North Arm than from the Main Arm. Sawmills using chlorophenols for wood preservation were implicated as the sources of chlorophenols.

Fish Kills

Kills of salmon attributable to wastewaters or chemicals have been reported in tributaries to the Fraser and

Thompson rivers on 23 occasions since 1959 (O. Langer, Department of Fisheries and Oceans, New Westminster, B.C., V3L 1B3, pers. comm.). Twenty-one of the reported kills occurred in creeks draining urban and suburban areas downstream of Hope. Juvenile coho (*O. kisutch*) were victims in 13 of the cases, chinook (*O. tshawytscha*) in three, and chum (*O. keta*) and sockeye in one case each. In some cases the species were not identified beyond *Oncorhynchus*. Mortalities were reported most frequently (three) in a creek which drains an industrialized urban area. Possibly the largest single loss occurred at Shuswap Lake in 1963 when "tens of thousands of juvenile sockeye" (IPSFC 1964) and possibly even more juvenile chinook were killed owing to an unauthorized application of DDT.

Adult salmon were reported killed in only one case and this occurred when ammonia was discharged to the Nicola River in August 1985, causing the death of approximately 111 mature chinook. Assuming equal proportion of males and females and a fecundity of 3 000 eggs per female (Fraser et al. 1982), the mortality represented about 170 000 eggs. In terms of potential fry production, the mortality of adult chinook salmon in the Nicola River was nearly as severe as the mortality of juvenile chinook in Shuswap Lake in 1963.

Some fish kills may not have been detected. Fish kills in large rivers would be difficult to detect because dead fish, which commonly sink, would be dispersed by currents. Furthermore, the natural turbidity of the Fraser River limits visibility so that dead fish would not be readily seen.

Juvenile chinook, believed to be of Fraser River origin, succumbed to low oxygen or became distressed at the surface and fell prey to birds on the intertidal foreshore area between the mouths of the North and Main Arms in 1980 (Birtwell et al. 1983). The condition was created by discharge of primary treated sewage from Iona STP into the intertidal zone. This discharge was relocated in 1988 to deep water in the Strait of Georgia.

Salmon Populations

Pink

Pink salmon spawning occurs within a few weeks after migrants enter the Fraser River in late August, September and October of odd-numbered years. Major spawning occurs in the mainstem Fraser between Chilliwack and Hope, in the Thompson River and in Seton Creek (Fig. 1). Spawning also occurs in large and small tributaries of the lower Fraser River. Fry emigrate to the Strait of Georgia upon emergence from spawning grounds in March to May.

In addition to wastewaters encountered during migrations of adults and fry, eggs spawned in the mainstem Fraser and Thompson rivers would be exposed to wastewaters during development from egg to fry when river flows were at their annual minimums. At 10-yr, 7-day low river flows, wastewaters would comprise about 2 % of total river flow in sections of the Thompson and Fraser rivers used for spawning (Table 3).

From 1959 to 1975 total runs of Fraser River pink salmon to the areas of commercial harvest varied widely in spite of total escapements ranging between one and two million (Fig. 4a). From 1977 onward, escapements were increased and total runs of pink salmon grew, with the exception of 1983. Escapements to mainstem Fraser spawning grounds increased steadily from a low in 1975 (Fig. 4b). Escapements to the Thompson River also rose from 1973 but declined in 1983 and 1985. However, observations in the Fraser Canyon (Hope to Lytton) in 1983 (Williams et al. 1986) and 1985 (IPSFC 1986) indicated that hydraulic conditions restricted passage to the upper reaches of the watershed, including the Thompson River. As a consequence, some pink salmon apparently dropped back to spawn in the mainstem Fraser. Between 1961 and 1985, an average of 74 % of the Fraser River pink salmon escapement spawned in the mainstem Fraser and Thompson River.

Because major wastewater discharges commenced in the interior of the Fraser watershed in December 1965, pink salmon population data are compared for periods preceding and following this date (Table 4). Total run size averaged 4.00 and 11.25 x 10^6, respectively in the periods before and after 1966 and were significantly different (Student's *t*-test; $P=0.05$, Simpson et al. 1960). The average number of effective female spawners was larger after 1966 than before but the difference was not significant ($P>0.05$). Average recruitment (ratio of total run to brood year effective female spawners) increased after 1966 but the difference was not significant ($P>0.05$). Starting with the 1961 brood, freshwater survival varied between nine and 18.7 % but there was no significant change between the periods preceding and following 1966 (IPSFC 1984; J. Woodey, Pacific Salmon Commission, Vancouver, B. C. V6E 1B9, pers. comm.) (Fig. 4c).

Owing to concern related to the abundance of benthic algae in the Thompson river, egg to fry survival was measured for the 1973 brood of pink salmon (Servizi 1976). Benthic algae were present on pink salmon spawning grounds of the Thompson River in autumn 1973 but were dislodged by spawners during redd formation, leaving a clean gravel surface. Algae gradually darkened the surface of redds but growth was minimal during winter. Algal abundance reached a maximum in March, 1974 just before pink salmon fry emergence. Based upon fecundity, spawning success and enumeration of fry using inclined plane traps, egg to fry survival was 27 % for the Thompson River. For all spawning populations of the 1973 pink salmon brood taken together, freshwater survival was 15.7 % (Fig. 4c).

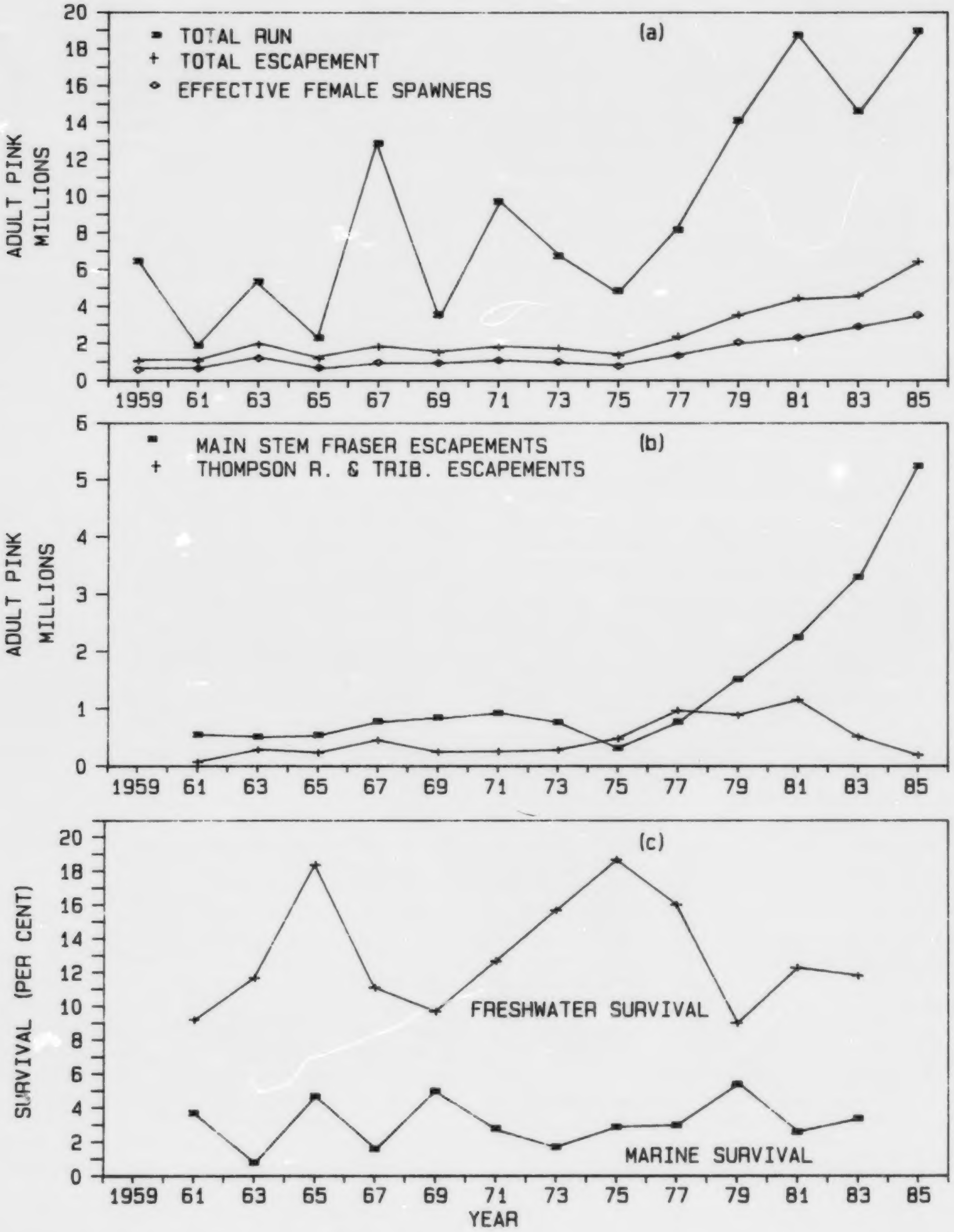

FIG. 4. Pink salmon run, escapement and survival since 1959. Data courtesy J. Woodey, Pacific Salmon Commission, Vancouver, B. C. V6E 1B9, pers. comm.

Thus it appears that benthic algae did not exert a negative impact on the 1973 pink salmon brood in the Thompson River.

The records of pink salmon run sizes, escapements, recruitments and freshwater survivals from 1967 onward cover 10, 2 yr cycles and show favorable trends for this species. Presumably, the amounts of treated wastewaters discharged to the Fraser River system did not preclude successful migration and spawning of pink salmon in the Fraser and Thompson rivers.

Sockeye

Sockeye salmon occur throughout the Fraser watershed (Fig. 1). The Fraser and Thompson rivers are used as migration pathways during July through October by adults returning to their natal streams. Most juvenile sockeye rear in lakes for 1 yr and smolts emigrate to the sea in April and May. A minor population rears in side channels of the lower Fraser River. Several major sockeye stocks on the Fraser system are characterized by a 4-yr cycle consisting of dominant, sub-dominant and two minor runs. Sockeye populations were severely depleted owing to obstructions to migration by slides in the Fraser River at Hell's Gate in 1912–14 and by overfishing. Since sockeye bound for the Fraser River were harvested in both Washington State and Canadian waters, the International Pacific Salmon Fisheries Commission was formed by a U.S.–Canada treaty in 1937 to protect, preserve and extend sockeye salmon of the Fraser River system. Data are available for total runs entering the areas of commercial harvest and for escapements to the spawning grounds since 1946. Data are grouped according to the quadrennial cycle years of 1910, 1911, 1912 and 1913.

The 1910, 12 and 13 cycles exhibited low points in 1962, 1964 and 1965, respectively, after which run sizes increased (Figs. 5a,c,d). The 1911 cycle exhibited uneven growth from 1945 onward (Fig. 5b). The 1910 cycle, dominated by the Adams River run which migrates into the Thompson River, reached 19 million fish in 1958 but declined sharply in 1962 owing to a number of factors, including apparently poor marine survival (IPSFC 1963). In June 1963, tens of thousands of juvenile sockeye from the 1962 Adams River spawning were killed by insecticide in rearing areas at Shuswap Lake (IPSFC 1964). This loss represented less than 0.03 % of the fry produced based on 1 063 000 spawners in Adams River, Little River and Scotch Creek, and historical averages; for spawning success (97 %), fecundity (4 272 eggs per female) and egg to fry survival (15 %) (Williams et al. 1987). In spite of the loss owing to insecticide, the total 1966 run increased relative to the prior cycle year (1962) and was larger than expected (IPSFC 1967). Thereafter, the total run on the 1910 cycle increased steadily to 16.7 million in 1986.

Sockeye population data are compared for periods prior to and following the commencement of major increases in wastewater discharges in December 1965. For each cycle, the means of total runs and effective female spawners was larger after 1965 than before but the difference was significant only for the 1911 cycle (Student's *t*-test; $P>0.05$) (Table 4). Mean recruitments were also larger for each cycle after 1965 than before but the difference was only significant for the 1912 cycle (Student's *t*-test; $P=0.05$).

A hypothetical study of pollution-caused mortality among sockeye was conducted in an attempt to describe the impact on population size (Brox 1976). Historical recruitment data for the Chilko race were incorporated into a mathematical model which superimposed pollution related mortalities during migration on natural mortalities. Twelve years of records for Chilko Lake sockeye showed that survival from smolt to adult ranged from about 2–22 % and was correlated with mean discharge of Chilko River during seaward migration of smolts (Williams 1969). Analysis indicated size of the average sustainable run would decrease owing to pollution-imposed mortalities (Brox 1976). Statistical

TABLE 4. Fraser River pink and sockeye salmon production; total runs, effective female spawners and recruitement.[a,c]

Species and cycle	Interval	Total run Mean x 10^6	Female spawners Mean x 10^6	Interval	Recruitment Mean
Pink	1959–65	4.00[b] (2.25)	0.79 (0.29)	1961–65	4.42 (3.33)
	1967–85	11.25[b] (5.48)	1.71 (0.97)	1969–85	7.49 (2.57)
Sockeye					
1910	1946–62	9.99 (6.27)	1.29 (0.49)	1950-62	8.67 (7.40)
1910	1966–86	10.06 (4.44)	1.31 (0.49)	1970–86	9.04 (1.60)
1911	1947–63	3.25[b] (1.31)	0.33[b] (0.11)	1951–63	11.11 (8.21)
1911	1967–83	5.97[b] (1.03)	0.53[b] (0.13)	1971–83	11.17 (3.30)
1912	1948–64	2.94 (0.67)	0.38 (0.12)	1952–64	6.75[b] (0.94)
1912	1968–84	3.99 (1.18)	0.40 (0.08)	1968–84	11.90[b] (3.16)
1913	1949–65	4.54 (1.16)	0.46 (0.16)	1953-65	10.52 (4.37)
1913	1969-85	7.84 (3.50)	0.61 (0.29)	1969–85	16.93 (3.84)

[a] () - equals standard deviation.
[b] Significant difference.
[c] Data courtesy J. Woodey, Pacific Salmon Commission, Vancouver, B.C. V6E 1B9, pers. comm.

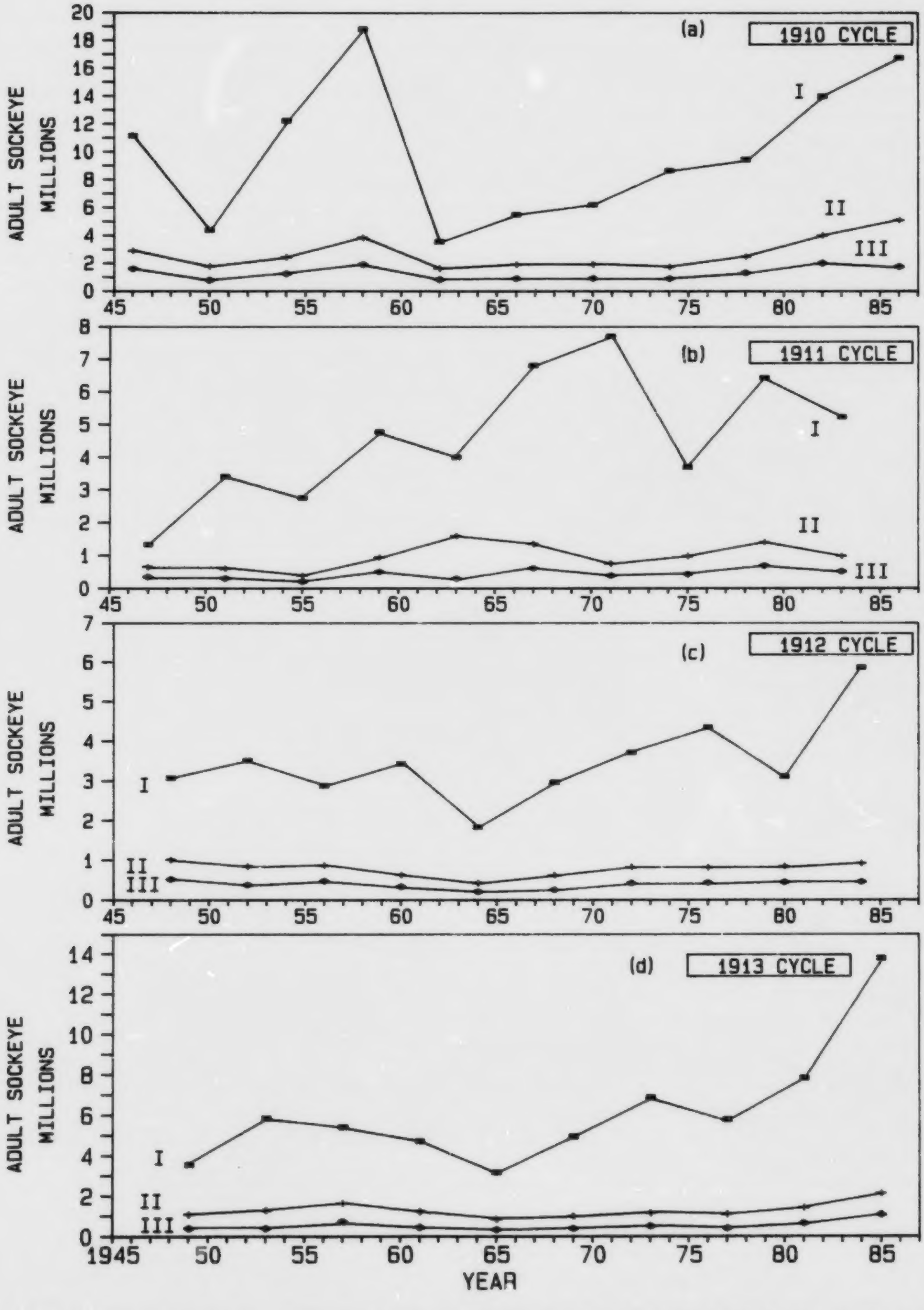

FIG. 5. Sockeye salmon total run (I) total escapement (II) and effective female spawner (III) for 1910, 1911, 1912 and 1913 cycles. Data courtesy J. Woodey, Pacific Salmon Commission, Vancouver, B. C. V6E 1B9, pers. comm.

variability about the mean was substantial due to variable natural mortality, and thus an impact on stock size would not be noted until several 4-yr cycles of pollution-caused mortalities had passed. The number of 4-yr cycles required to produce results was not determined.

The records of total runs, effective female spawners and recruitments reveal nothing to suggest a negative trend since major additions of wastewater commenced in late 1965. However, since 1965 each race of sockeye salmon experienced only five, 4-yr cycles, except the 1910 cycle races which experienced six. Furthermore, since negative impacts may not be noticeable at the population level until several 4-yr cycles have passed, it is imperative that comprehensive population data be obtained on a continuing basis.

Chum

Chum salmon spawning runs occur annually from September to January in the Fraser River and tributaries downstream of Hell's Gate. Palmer (1972) reported that approximately 20 % of chum salmon may spawn in tributaries (Fig. 1). Recent estimates indicate that approximately 2 % of chum salmon spawn in the Fraser mainstem (Farwell et al. 1987). Eggs develop during winter; fry emerge in March through May and emigrate to the Strait of Georgia. Some chum salmon fry rear briefly in the inner estuary of the Fraser River (Levy and Northcote 1982).

Chum salmon returning to the Fraser River are harvested with other stocks. The accuracy of spawning escapements has been questioned (Peterson and Lewynsky 1985). In addition, Beacham (1984) concluded that: (1) an accurate measure of production from the Fraser River is not available; (2) Fraser River chum salmon stocks have varied widely in apparent response to changes in harvest rates; and (3) rehabilitation of chum salmon stocks requires reduction and stabilization of harvest rates. Harvest rates have been reduced since 1983 (M. Farwell, Department of Fisheries and Oceans, New Westminster, B. C. V3L 1B3, pers. comm.). As a consequence of these factors, it is not possible to determine whether wastewaters exacerbated declines in stock size attributed to harvest rates.

In spite of the limited data base, a survey of records (Department of Fisheries and Oceans) for chum salmon spawning streams was undertaken to determine whether apparent declines in stocks could be linked to catch and habitat condition (Peterson and Lewynsky 1985). This analysis indicated no correlation between spawner escapements and wastewater discharges. Finally, the portion of the chum salmon population which spawns in the mainstem Fraser does so in the same general area as pink salmon. However, recent observations in the mainstem indicate chum salmon concentrate spawning near ground water sources (M. Farwell, ibid, pers. comm.). Since mainstem pink salmon numbers were apparently unaffected by wastewater, it is possible that mainstem Fraser chum salmon numbers would not have been affected.

Coho

Adult coho salmon are 3-4 yr of age when they enter the Fraser River in September and October bound for approximately 150 spawning streams in the southern half of the Fraser River system (Fig. 1). Many of the smaller tributaries are selected and spawning may occur over several months (Fraser et al. 1982). Coho are not known to spawn in the mainstems of the Fraser or Thompson rivers. Fry emerge in spring and juveniles generally spend one year in freshwater before emigrating to the ocean. Coho commonly overwinter in tributary streams, side channels and marshes.

The annual size of coho stocks is poorly known because it has not been possible to measure overall ocean harvest rates and escapement data are believed unreliable (Fraser et al. 1982). However, long-term declines in escapements of some stocks were attributed to over exploitation and habitat deterioration but the role of each could not be assessed (Fraser et al. 1982). More recently, long-term declines in escapements and harvest rates in excess of optima have been documented (Anon. 1986c).

Although the majority of wastewaters are discharged to the Fraser and Thompson rivers, several smaller streams, especially near urban and farming areas, receive wastewaters, stormwaters and contaminants from direct discharge and non-point sources. In some cases contaminants have reached acutely toxic levels leading to fish kills. Since coho utilize these small streams, they are the species of salmon most commonly killed. Juvenile coho were victims on 13 of 21 occasions when salmon were killed in small, urban streams. Eleven of 60 streams with coho populations in the lower Fraser basin were judged to have water contamination severe enough to affect fish production, but there was inadequate escapement data of good quality to make an assessment of possible impact on the population (Peterson and Lewynsky 1985). It is possible that the effects of contaminants on coho stocks may be greater than can be verified by existing population data.

Chinook

Most adult chinook salmon are 4-5 yr of age when they enter the Fraser River in February through October (Fraser et al. 1982). Chinook spawn in about 65 tributaries throughout the Fraser River basin (Fig. 1). Fry stay from a few weeks to 1 or 2 yr in freshwater before emigrating to the sea. The full extent of freshwater residence of juvenile chinook has yet to be determined. Studies indicate some juvenile chinook leave their natal streams and take up residence in the Fraser River (Tutty and Yole 1978), including inner estuarial areas (Levy and Northcote 1982). Some juvenile chinook occur throughout the inner estuary from late February to late July (Birtwell et al. 1981). Juvenile chinook were found upstream and downstream of pulp mill effluent diffusers at Prince George in October 1980 (G. Derksen, Environmental Protection, West Vancouver, B.C., V7T 1A2, pers. comm.). Juvenile chinook were also detected in the Fraser River downstream of Prince George and in the Thompson River in August 1984 (Levings et al. 1985). Recently, overwintering populations of juvenile chinook have been detected in the Fraser River near Prince George, Quesnel, Lytton and Agassiz (Whelen and Slaney 1986). Juvenile chinook have also been observed to overwinter in the Thompson River (Whelen and Slaney 1986).

Analysis of chinook stocks is complicated because actual catches are largely unknown for Fraser River chinook except for some hatchery stocks, a few wild stocks and the terminal harvest. In addition, the quality of escapement data is inconsistent since methodology varies from one area to another and data are subject to a variable sampling bias (Fraser et al. 1982). A test fishery in the lower Fraser River has provided a more realistic indicator of relative escapements since 1980. In spite of these shortcomings, these authors concluded that total returns of chinook to the mouth of the Fraser River showed a strong decline from 1970 to 1981 which was attributed primarily to increased harvest prior to the terminal fishery. There are insufficient data to determine whether wastewater discharges exacerbated this decline. Strong recoveries in returns of Chinook to the Fraser were noted in 1984, 1985 and 1986 owing to restrictions on commercial, native and sport harvests. (N. Schubert, Department of Fisheries and Oceans, New Westminster, B.C., V3L 1B3, pers. comm.).

As a consequence of the foregoing factors, an overall assessment of possible effects of wastewaters on chinook stocks is not feasible, but limited analysis was attempted. An examination of escapement and catch records was made for chinook stocks spawning in tributaries of the lower Fraser to determine if stock declines could be linked to catch and habitat condition (Peterson and Lewynsky 1985). These authors concluded that five stocks of chinook salmon in the lower Fraser showed declining trends but the declines were not correlated with significant habitat impairment in the natal stream. It is possible that the declines were due to unequal harvest of returning adults. On the other hand, the study did not consider possible impacts owing to wastewaters in the Fraser River, where juvenile chinook may spend extended periods.

Isolated events led to significant mortalities of juvenile and adult chinook. At least tens of thousands of juvenile chinook salmon were killed when insecticide was sprayed at Shuswap Lake in June 1963. Although no declines in escapements to the spawning grounds tributary to Shuswap Lake were observed in 1966 and 1967, the population data are not good enough to support a conclusion that there was no adverse impact. In another case, approximately 111 mature chinook were killed by an ammonia discharge to the Nicola River in August 1985. This represented approximately 2 % of the spawning population (N. Schubert, Department of Fisheries and Oceans, New Westminster, B.C., V3L 1B3, pers. comm.). The subsequent impact would be observed in returning runs in 1988–90 but is likely to be masked by enhancement programs in the system.

The populations of juvenile chinook which overwinter in the Thompson and upper Fraser Rivers do so when flows and water temperatures are at annual minimums (Whelen and Slaney 1986). Wastewater concentrations in the Fraser River could exceed three per cent upstream of Prince George (Table 1) at 10-yr, 7-day average low flows and would be in the range of 2-3 % between Prince George and Quesnel and near 2 % in the Thompson River. In dilution zones near pulp mills, treated effluent concentrations would be greater. Kovacs (1986) estimated the threshold of sublethal effect of ''raw'' and biologically treated bleached kraft pulp mill effluents as approximately 2 and 4 %, respectively. Thus there is significant potential for impact on overwintering juvenile chinook. The risk of sublethal effects is further increased because preliminary data indicate that even slightly elevated temperatures may attract juvenile chinook into dilution zones during winter (C. Levings, Department of Fisheries and Oceans, West Vancouver, B.C., V7V 1N6, pers. comm.). Although temperature profiles have not been reported for winter conditions, measurements at one pulp mill diffuser upstream of Prince George in May revealed increases of 0.30° and 0.18°C at 270 and 550 m, respectively, downstream of the diffuser at a river flow of 81 400 x 10^3 m^3 d^{-1} (Anon. 1980). Temperature increases downstream may be greater in winter than those measured in May, since treated wastewaters discharged by pulp mills would have temperatures in the range 20–25°C (Anon. 1984), while the Fraser River would be near 0°C (Whelen and Slaney 1986), at a mean January flow of 15 500 x 10^3 m^3 d^{-1} (Anon. 1985). Since biologically treated pulp mill effluents contain residual contaminants, including chlorinated phenolics, the implications for energy metabolism and survival of juvenile chinook requires further study.

There is also potential for impact on juvenile chinook in lower reaches of the Fraser River. Some juvenile chinook rear in the inner estuary of the Fraser River for a few weeks where industrial and major municipal discharges occur. Discharges from various sites plus multiple dosing due to river flow reversal under certain tidal conditions may create temperature profiles which attract juvenile salmon into dilution zones. Near Annacis Island STP, multiple dosing associated with 50–30 h of slack water per month between January and May (Narayanan 1980) may create wastewater concentrations ranging between 0.6 and 25 % (Anon. 1979). The implications for juvenile chinook of these discharges require further study.

Discussion

To assess whether wastewater criteria applied by Federal and Provincial agencies have successfully protected Fraser River salmon, various historic data were examined. Wastewaters discharged to the upper Fraser River system, the Thompson system and the total Fraser have increased 38, 12 and 3-fold, respectively, since 1965 (Fig. 3). Pulp mill effluents, which received secondary treatment from the outset, were the principal new sources of effluents. All wastewaters were required to meet effluent toxicity objectives (Table 1). However, four discharges (Quesnel River Pulp Co. Ltd., Belkin Inc., Annacis Island STP and Lulu Island STP) which comprise about 23 % of total wastewaters, have yet to be upgrated to meet Level A. Wastewater monitoring data indicated that toxicity objectives were not always met, but frequency of compliance improved as treatment facilities were upgraded. Calculations indicated potential for sublethal stress on salmon downstream of the three pulp mills at Prince George during low flow in April 1977 (Anon. 1984). Unsafe conditions for fish may occur at times in the dilution zone at Annacis Island STP due to multiple dosing at low river flows (Singleton 1980).Surveys in the Fraser and Thompson rivers of benthic invertebrates indicated responses ranging from "no-effect" to "organic enrichment" and "alteration of diversity" toward more pollution tolerant forms.

Population data for sockeye and pink salmon revealed that stocks of these two species have increased since about 1965 presumably owing to a favorable combination of management to re-build stocks, natural environmental factors and enhancement. Presumably, treated wastewaters did not preclude successful migration of these two species or spawning of pink salmon in the mainstems of the Fraser and Thompson rivers. For chum, coho and chinook the data were not adequate to differentiate possible impacts of wastewaters from other habitat impacts or natural, enhancement and management factors which affect population size.

A note of caution is warranted concerning overwinter rearing areas and spawning grounds in the Fraser and Thompson rivers since wastewaters could comprise 2 % or more of total river flow (Table 3). Although the wastewaters include more than pulp mill effluents, the latter constitute about 79 % of the total and all contain residual contaminants. Kovacs (1986) estimated the threshold of sublethal effects of "raw" and biologically detoxified bleached kraft pulp mill effluents as approximately 2 and 4 %, respectively. Thus, relaxation of effluent criteria, increases in wastewater discharges or lower winter river flows (IPSFC 1983) may have serious consequences for all salmon, and especially for chinook, pink and chum salmon which are present in the mainstem Fraser and Thompson rivers throughout the winter low flow period.

Outright kills of salmon occurred in some tributaries and these were usually caused by substandard discharges or unauthorized activities (i.e. pesticide application). There were indications that pollutants are affecting salmon stocks, especially coho, in some small, urban streams. Owing to small flows in these streams, a much higher standard of wastewaters treatment or prohibition of wastewaters discharge, even though treated, may be the only means of protecting these stocks.

The extent to which juvenile chinook rear in the Fraser River was poorly documented when wastewater criteria were adopted by regulatory bodies. Since recent data indicate some populations of this species spend considerable time in the vicinity of major wastewater discharges, it appears that specifying detoxification of wastewaters before discharge was prudent. However, a recent review (McLeay et al. 1986, p. xxiii), concluded that sublethal toxic effects or long-term consequences for indigenous aquatic species cannot be derived from the acute lethal bioassay on which effluent Objectives (Table 1) are based. Furthermore, analysis in an earlier section of this report revealed significant potential for impact on juvenile chinook resident in the Fraser and Thompson Rivers, especially near dilution zones. Protection is vital to programs established to rebuild salmon stocks through management and enhancement. Accordingly, further research is required to determine the level of protection required.

The Fraser River is an example, possibly the first, of wastewater toxicity criteria being applied on a major river system in advance of significant industrialization or measurable impact on aquatic resources. It cannot be determined what the impact on Fraser River salmon might have been if effluent objectives, including toxicity criteria, had not been applied. Based on experiences at other major industrialized rivers in the world, salmon stocks would probably have fared poorly in the Fraser in the absence of wastewater toxicity criteria.

Industry and various levels of government incur costs associated with wastewater treatment. However, imposition of effluent criteria has apparently not limited industrialization or population growth on the Fraser system. For example, the pulp and paper industry, which discharges most of the wastewater, has expanded from approximately 330 t d^{-1} in late 1965 to about

5 830 t^{-1} in 1985 with various proposals for further expansion (G. Tanner, Environmental Protection, West Vancouver, B.C., V7T 1A2, pers. comm.). Human population on the Fraser River basin increased approximately 80 % between 1967 and 1981 (Anon. 1968; Anon. 1982).

If salmon resources are to prosper in future, the level of protection must keep pace with growth in industry and population. Owing to variability in freshwater and marine survival, several years may pass before an impact on salmon stocks owing to wastewaters would become identifiable at the population level. Regulatory bodies would be ill-advised to allow wastewaters to reach the level of impact before corrective action is taken. Irreplaceable salmon stocks could be lost in the process. This may mean upgrading wastewater treatment or restricting discharges at some future time since the capacity of the Fraser system to accept contaminants and support major salmon runs must be considered finite. In the case of some smaller tributary streams this capacity may have already been exceeded. For its part, the Department of Fisheries and Oceans should obtain adequate population data to differentiate the impact of pollutants and habitat deterioration on salmon stocks from natural environmental factors, enhancement and management practices. Special emphasis should be placed on upgrading population data for coho, chum and chinook, including measurements of freshwater survival. At the same time it is the responsibility of scientists to produce the knowledge on which protection can be based. For example, Ongley (1986) recommends development of sophisticated bioassay techniques which provide objective information from which environmental managers can make judgements about the potential for ecological hazard and risk in aquatic systems.

Conclusions

1. Discharges of wastewaters to the Fraser River system overall have increased 3-fold since 1965. Increases were 38 and 12-fold to the upper Fraser and Thompson rivers, respectively.
2. Approximately 77 % of wastewaters meet British Columbia Level A Objectives for toxicity.
3. Stocks of Fraser River sockeye and pink salmon have increased since about 1965. There was no indication that treated wastewaters precluded successful migration of these two species in spring through autumn or spawning of pink salmon in the main stems of the Fraser and Thompson rivers.
4. The data for chum, coho and chinook were not adequate to differentiate possible impacts of wastewaters from other habitat impacts, or natural and management factors which affect population size.
5. There were indications that salmon stocks, especially coho, in some small, urban streams, are at risk owing to pollutants.
6. There is significant potential for wastewater impact on juvenile chinook salmon resident in the Fraser and Thompson rivers, especially near dilution zones.
7. Elevated wastewater concentrations during low flow periods, increases in wastewater volumes, relaxation of detoxification criteria or reductions in river flow could have serious consequences for pink, chum and juvenile chinook salmon resident in the mainstem Fraser and Thompson rivers during winter.
8. For future assessment, it is recommended that the Department of Fisheries and Oceans at least maintain the quality and extent of data which exists for sockeye and pink salmon while upgrading data for chum, coho and chinook, including measurements of freshwater survival.
9. Research is needed to define potential impacts of mixtures of residual pollutants on salmon and the level of protection required to protect salmon stocks.

Acknowledgments

The author acknowledges the efforts of the following persons who made helpful suggestions and assisted by compiling records from their files. George Derksen and Gerald Tanner (Environmental Protection); Norman Eckstein, Kris Andrews, Dave Brown, Kenneth Evans and Harold Vogt (B.C. Waste Management Branch); Brian Talbot (Greater Vancouver Regional District); James Woodey (Pacific Salmon Commission); Wayne Saito, Neil Schubert, Morley Farwell, Michael Nassichuk and Steven Samis (Department of Fisheries and Oceans).

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The Impact of Habitat Damage on Atlantic Salmon (*Salmo salar*) Catches

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Abstract

WATT, W. D. 1989. The impact of habitat damage on Atlantic salmon (*Salmo salar*) catches, p. 154–163. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

The status of Atlantic salmon (*Salmo salar*) habitat is reflected in the long-term catch trends, wherever the catch can be related to specific habitat areas. When impact frequencies are low, short-term habitat damage does not noticeably affect the long-term catch trend. When the frequency of short-term impacts is high (chronic) and where the damage is irreversible there can be a significant impact on the catch trend. However, the catch record also reflects short-term stock-recruitment features, and other long-term effects not related to habitat alteration. An estimate of the long-term change in productive capacity of Canada's Atlantic salmon habitat was obtained from the annual catch record of Canada's commercial salmon fishery, corrected for the effects of large-scale short-term events and the long-term trends common to all of the salmon fishery. The productive capacity of Atlantic salmon habitat in Canada has declined 17 ± 5 % since 1870. The extent of known salmon habitat losses and gains in eastern Canada since Confederation accounts for approximately a 16 % loss in productive capacity, which compares quite well with the observed long-term decline in yield.

Résumé

WATT, W. D. 1989. The impact of habitat damage on Atlantic salmon (*Salmo salar*) catches, p. 154–163. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Les tendances à long terme des captures de saumons de l'Atlantique (*Salmo salar*) reflètent l'état de leurs habitats, dans les cas où l'on peut établir un lien entre les captures et des habitats précis. Lorsque les perturbations sont peu fréquentes, les dégâts causés à court terme n'influent pas de façon notable sur les tendances à long terme des captures. Les perturbations à court terme (chroniques) fréquentes et les dommages irréversibles peuvent influer de façon marquée sur la tendance des captures. Toutefois, les registres de captures reflètent également les caractéristiques stocks-recrues à court terme et d'autres effets à long terme non liés à la dégradation des habitats. On a estimé les changements à long terme de la capacité de production des habitats du saumon de l'Atlantique au Canada d'après les captures annuelles des pêcheurs de saumons commerciaux canadiens, données qui ont été corrigées pour tenir compte des effets des événements d'envergure à court terme et des tendances à long terme propres à toutes les zones de pêche du saumon. Depuis 1870, la capacité de production des habitats du saumon de l'Atlantique au Canada a diminué de 17 ± 5 %. L'importance des pertes et des gains connus à l'égard des habitats du saumon dans l'est du Canada depuis la Confédération correspond à une perte d'environ 16 % de la capacité de production, ce qui est tout à fait conforme aux diminutions de la production observées à long terme.

Introduction

Canada's Atlantic salmon fishery is commonly perceived as a fragile resource, subject to overexploitation (which has led to stock/recruitment problems) and vulnerable to environmental degradation (which has reduced the stock base by destruction of salmon rearing habitat). The major problem of concern to the Department of Fisheries and Oceans and to Canadian fishermen is the impact of the above on the yield to the various Atlantic salmon fisheries. It is desirable to maintain salmon production (catch) at a high but stable and sustainable level, and to protect the habitat base that supports the sustainable yield.

Both the stock/recruitment and the habitat destruction problems are expected to decrease the yield to the Atlantic salmon fishery, but they should affect it in somewhat different ways. Most stock/recruitment problems related to overfishing can be expected to have an effective time scale in the order of 10 yr due to the 4–6-yr generation time of Atlantic salmon. Most habitat destruction problems have much longer term impacts on yield.

Damage to Atlantic salmon habitat can be both natural and anthropogenic. Natural damage would include that inflicted by floods, landslides and some soil erosion. In actual practice the distinction is blurred, because much "natural" damage has an underlying anthropogenic cause, e.g., forest clearing promotes floods and agricultural practices promote soil sheet erosion.

Short-Term Habitat Damage

Anthropogenic damage to Atlantic salmon habitat can be classified as short-term (< 10 yr), chronic, and long-term. Short-term damage, such as chemical spills and siltation from construction sites, is repaired by natural environmental processes. Unless the frequency of short-term environmental damage is high, there can be no long-term impact on salmon production.

A notorious example of massive, but short-term, damage to Atlantic salmon habitat is the DDT spraying of New Brunswick forests in the 1950's. Figure 1 shows the normalized (divided by the mean) annual angling catch for five unobstructed New Brunswick rivers in whose drainage basins the principal industrial activity is forest harvesting, and the normalized commercial Atlantic salmon catch from Restigouche and Northumberland Counties is northeast New Brunswick. Heavy DDT spraying (0.5–1 kg·ha^{-1}) occurred in the years 1952 to 1958 (MacDonald 1965). (DDT spraying continued at a reduced rate from 1960 to 1965, with special efforts being made to avoid spraying watercourses.) Assuming a 5-yr life cycle for New Brunswick salmon, the impact of the initial spraying (1952) on catches should have occurred over the period 1954 to 1956, and from the last heavy DDT spraying (1958) impact would be expected over the period 1960 to 1962. Taking the middle years for onset and end of the major impact period, we can compare the mean catch during the period 1955 to 1961 with catches before and after. For the commercial catches of Northumberland and Restigouche Counties, the 7 years of spraying impact were compared to the 7 preceeding years (1948–54) and the 7 following years (1962–68). For angling data, only 4 years of data are available prior to the spray impact period, and nine post spray years. Angling data after 1970 were not used because of the higher angling catches that resulted after the commercial salmon fishery was curtailed. In both angling and commercial catch comparisons (two way analysis of variance, using a logarithmic transformation to correct for heteroscedasticity) the means for the period from 1955 to 1961 were significantly lower ($P<0.001$) than pre-impact and post-impact catches. The catch records of Fig. 1 suggest that a full recovery occurred six years after heavy DDT spraying ceased.

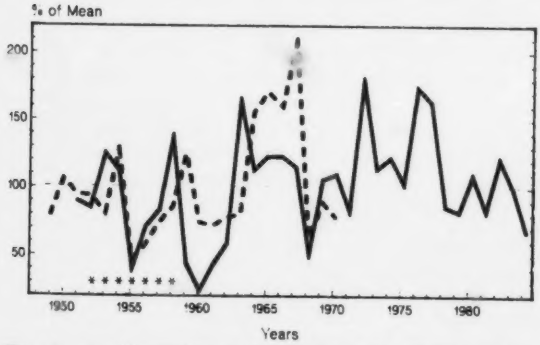


FIG. 1. An illustration of the impact of the DDT spraying of New Brunswick forests (for control of spruce budworm) on Atlantic salmon catches. The solid line is the mean normalized annual angling catch from five unobstructed New Brunswick rivers (Jacquet, Restigouche, Miramichi, Kennebecasis and Nashwaak), and the dashed line is the normalized annual commercial catch from Restigouche and Northumberland counties, New Brunswick. The asterisks indicate years of heavy DDT spraying. The angling data were taken from Smith (1981) and Swetnam and O'Neil (1984). The commercial data were compiled from «Fisheries Statistics of Canada», published annually by Statistics Canada, Ottawa.

The more common short-term impacts are the result of erosion and siltation from streamside construction sites, most notably bridges and culverts. Siltation at these sites results from using poor construction practices, or from natural susceptibility of easily erodable soils and/or weather conditions unfavourable to rapid regrowth of ground-cover plants (after hydroseeding). Recent development of better construction practice guidelines and specifications should help to alleviate habitat damage through ignorance, but in some environments the soil is so susceptible to rapid erosion that even the best practicable technology is inadequate.

Other common causes of habitat damage include excavation of pools to improve local angling, use of instream gravel for short-term erosion control measures, in-stream gravel mining (which occurs on both small and large scales), and stream channelization, which effectively converts the stream into a drainage channel (usually for flood control). Localized physical alterations of this sort, involving changes in the streambed grade, which natural processes will gradually restore, cannot affect salmon production in the long term. Even stream channelization, which can result in massive initial impact on juvenile Atlantic salmon production, has a recovery period (unless the channel is continuously maintained) in the order of 5–10 yr (J. R. Semple, P. G. Zamora, and R. Rutherford, Dep. Fisheries & Oceans, Halifax, N.S., unpublished data)

A number of available examples indicate the lack of long-term impact on salmon production from these types of activity, especially in those areas where anthropogenic input is mainly limited to forest harvesting (e.g., Iwanaga and Hall 1973; Ringler and Hall 1975; and Harr and McCorison 1979). Studies in Atlantic Canada, notably the Nashwaak Watershed

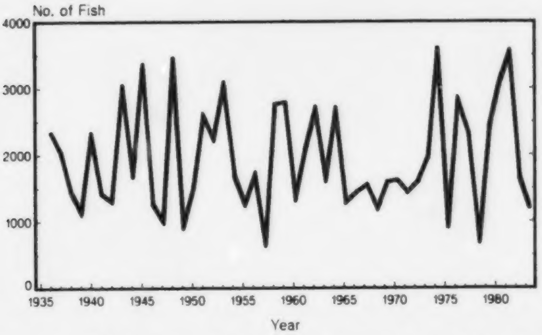


FIG. 2. Total (summed) annual angling catch from 12 unobstructed and unacidified ($pH>5$) mainland Nova Scotia salmon rivers. For the years 1936 to 1950 the data were compiled by MacEachern and MacDonald (1962), from the annual reports of fishery officers. Data for the years 1951 to 1979 are from Smith (1981), and 1980 to 1983 are from Swetnam and O'Neil (1984).

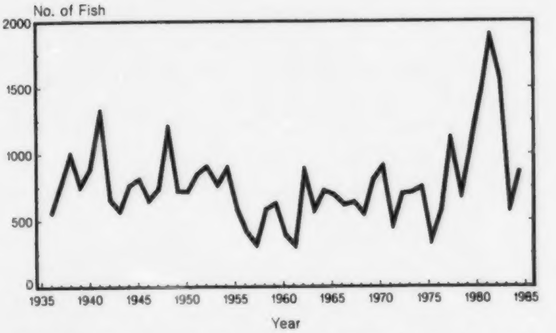


FIG. 3. Summed annual angling catch from six unobstructed salmon rivers on Cape Breton Island, Nova Scotia (Baddeck, Cheticamp, Grand, Margaree, Middle, and North). The data sources are the same as those for Fig. 2.

Study in New Brunswick, and studies reported by Henderson (1978), Case and Donnelly (1979), Hall (1980), Englert et al. (1982) and Grant et al. (1986), have indicated that forest road (and skidder trail) construction practices, particularly at stream crossings, present the only measurable deleterious impact of present-day forest harvesting practices on salmon habitat (though clearcutting may sometimes result in short-term enhancement of juvenile Atlantic salmon production, Englert et al. 1982, and Grant et al. 1986).

Areas where anthropogenic impact is limited to forest harvesting activity can serve as controls against which the impact of long-term habitat degradation can be measured. Notable examples of catch records that suggest minimal habitat disruption are the angling records of twelve unacidified ($pH>5$) salmon rivers along the Atlantic coast of mainland Nova Scotia (Fig. 2). Most of the southern Nova Scotia forest cover is still much the same as it was in the 1930's, and the twelve rivers represented in Fig. 2 still yield the same total number of salmon to the angling fishery as they did half a century ago. Watt et al. (1983) reported that, when examined individually, the angling records from ten of the twelve rivers show no significant trend in angling success since 1936, and of the other two, one shows an increase and the other a decline. When the data are combined into a variance analysis there is no significant long-term trend ($P>0.4$). A similar picture (Fig. 3) appears in the angling records of six unobstructed Atlantic salmon rivers on Nova Scotia's Cape Breton Island. The notable peak in angling success in 1981–82 occurred on all six of these Cape Breton rivers, apparently as a result of the 1981 curtailing of a portion of the Newfoundland commercial salmon fishery that intercepted returns to Cape Breton rivers. A hatchery stocking program on the Margaree has also contributed to increased catches from that river. Even with the 1981–82 peak included, the data show no significant trend over the half century ($P>0.2$).

For most of eastern Canada, a continuous record of commercial salmon fishery landings, by county, is available back to 1870, compiled by Dunfield (1985; Dep. Fisheries and Oceans, Halifax, N.S., unpubl. data) from the annual reports of the Department of Marine and Fisheries and the journals of the houses of assembly of Prince Edward Island and Newfoundland; and from "Fisheries Statistics of Canada", published annually by Statistics Canada, Ottawa; and by May and Lear (1971). Probably the best long-term record from an area of negligible habitat degradation is the commercial fishery record of Northumberland County, New Brunswick. Most commercial fishery records are not interpretable into habitat terms because most commercial salmon fisheries are multistock interception fisheries and do not reflect the habitat status of any single river or area. Three Maritime commercial fisheries are mainly terminal in nature, and one of these is the Northumberland County fisheries which exploit the Miramichi Bay stocks. The record of this fishery since confederation is depicted in Fig. 4. The two periods of

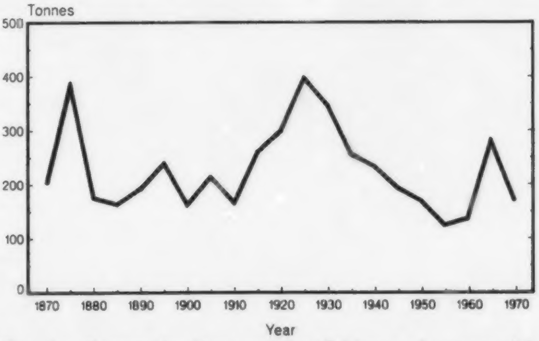


FIG. 4. Consecutive 5 yr averages of the annual commercial Atlantic salmon catch in Northumberland County, New Brunswick.

historical highs are correlated with increased effort which may have caused the subsequent stock/recruitment problems. The low catches in the late 1950's correlate well with DDT spraying. But the overall record for a century shows no statistically significant trend ($P > 0.4$, t-test).

Chronic Habitat Damage

When the number of short-term impacts is high, salmon habitat damage becomes chronic, and the effect on Atlantic salmon production becomes long-term, which impacts negatively on the landings record. An example of apparent chronic habitat destruction is available from the Restigouche River, New Brunswick, where river driving of logs persisted into the 1970's and, since the 1940's, the river driving was accompanied by an annual river channelization to clear the route. Such chronic habitat damage can be expected to show in the commercial salmon landings for Restigouche County, New Brunswick. This fishery exploits stocks from a number of Chaleur Bay rivers, but the major stock group is from the Restigouche River. In contrast to the lack of long term trend in the adjacent commercial fishery of Northumberland County (Fig. 4), the Restigouche County commercial salmon landings record shows a significant decline in landings in recent decades ($P < 0.01$, Fig. 5), which can be attributed to chronic habitat destruction. Discontinuation of the annual river channelization work in the early 1970's (coincident with introduction of habitat clauses into the Fisheries Act in 1973) should have led to recovery within 5–10 yr. This effect does not show in the commercial data record for Restigouche County, because the Department of Fisheries and Oceans imposed a ban on commercial salmon fishing in 1971.

More-extreme examples of chronic damage are available from areas of intensive agriculture. Soils suitable for intensive agriculture are, by nature of their suitability, very susceptible to erosion. Because of their high silt and/or clay content, erosion of these soils is particularly damaging to salmon habitat. Such soils are found in the Maritimes wherever geology is Carboniferous or later (excluding basalts and other lava flows). Susceptible soil areas include much of northern Nova Scotia, southeast New Brunswick, parts of northern New Brunswick, and all of Prince Edward Island. Soils of this type are rare in Newfoundland, and farther north there is no agricultural activity to disturb them.

An example of the impact of long-term chronic habitat degradation from agriculture is afforded by the commercial salmon fishing record for Hants County, Nova Scotia. This is another terminal commercial fishery, where the exploited stocks are those of the Minas Basin rivers, and the long-term commercial landings record can be taken as an indication of the health of these stocks. Long-term decline of the Minas Basin stocks, to about 10% of their level a century ago, is apparent from Fig. 6 ($P < 0.001$). Urbanization has probably also played a role in chronic habitat degradation of the Minas Basin rivers.

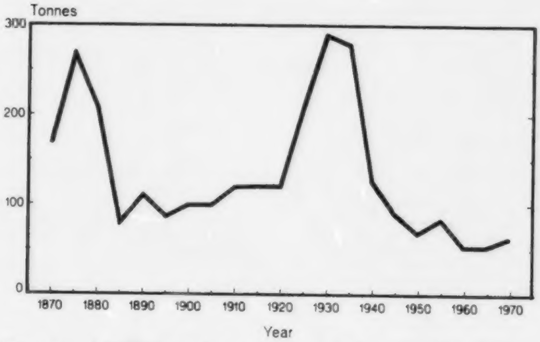
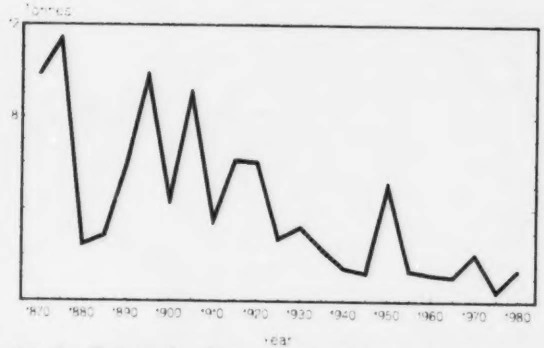


FIG. 5. Consecutive 5-yr averages of the annual commercial Atlantic salmon catch in Restigouche County, New Brunswick. The river has been channelized annually since the 1940's, to facilitate log driving.



IG. 6. Consecutive 5-yr averages of the annual commer-ial Atlantic salmon catch in Hants County, N.S. The salmon abitat in this area has been heavily impacted by agricultural evelopment.

Another example of severe chronic salmon habitat degradation is the acidification of Nova Scotian rivers. Watt (1986) has calculated that one-third of Nova Scotia's available salmon habitat has been lost to acidification since 1950, representing an average reduction of 12,000 fish in annual Canadian salmon landings. Habitat damage from acidification goes beyond chronic degradation in 13 rivers where the salmon runs have apparently been extirpated (Watt et al. 1983). Even if acid deposition could be stopped and the habitat allowed to purge itself, short-term natural recovery of these salmon stocks is no longer possible.

Long-Term Habitat Damage

Long-term destruction of Atlantic salmon habitat results when the river is given over to uses which compete directly with salmon production. In eastern Canada, the conflict at present is usually with hydroelectric power development. Historically, however, dams were employed on many rivers for direct water power to operate mills (e.g., the St. Croix River, Maine/New Brunswick) and to create impoundments for other purposes. Dams are also employed for flood control and for highway crossings (Petitcodiac River, N.B.; Annapolis River, N.S.; and Middle and West rivers, Pictou County, N.S.). Fishways can only partially mitigate the fish passage problems imposed by dams; even the best upstream fish passage systems cannot be 100 % efficient.

Data on upstream fish passage efficiencies for Atlantic salmon at fishways are available for three fishways on the Saint John River in New Brunswick, for three fishways on the St. Croix River, New Brunswick/Maine, and for one fishway at Sheet Harbour in Nova Scotia. J. R. Semple (Dep. of Fisheries and Oceans, 555 W. Hastings Street, Vancouver, B.C. V6B 5G3, unpubl. data) released a total of 136 tagged salmon and grilse of mixed wild and hatchery origin at a release site five kilometers below Mactaquac Dam (lowest dam on the Saint John River system) in 1976. The recovery rate was 71 %. When only wild fish are considered (30 salmon) the recovery rate at the Mactaquac fishway trap was 83 %. A similar study, reported by Watt (1988) was carried out at the Milltown dam on the St. Croix River. Eighteen tagged fish were released in the estuary, and the recovery rate at the Milltown fishway was 72 %. Brawn (1972), conducting a sonic tag study of salmon behaviour in Sheet Harbour estuary, trapped and tagged 16 fish in the estuary and recovered eleven of these at the fishway for an efficiency of 69 %. More data are available for upriver fishways. For Beechwood dam on the Saint John River, data from 1976 to 1982, reported by Ingram (1981, 1987), indicate that of a total estimated release of 23 500 wild salmon and grilse (corrected for angling) below Beechwood, 17 200 were recaptured in the Beechwood fishway trap for a mean fish-passage efficiency of 73 %. Data for an estimate of fish-passage efficiency at Tobique Dam are available from Ingram (1984) and Francis (1984). Over the period from 1978 to 1982, 12 000 wild salmon and grilse were released from Beechwood fishway and 4600 of these were recaptured in the Tobique fishway trap, giving a mean fish-passage efficiency of 38 %. The fish-passage efficiency estimates for Beechwood and Tobique must be considered minimal because no allowance has been made for natural mortality (thought to be negligable) or for some of the fish homing to rearing habitat below the fishways. With regard to this latter source of error, Watt and Penny (1980) have shown that most wild returns to Mactaquac dam are the progeny of fish that spawned in the Tobique River tributary, so this error too is not likely to be large. For the St. Croix River, Watt (1988) reports a mean fish-passage efficiency of 55 % for the Woodland dam fishway in 1985 and 1986, and 50 % for the fishway at the Grand Falls dam.

Similarly, the efficiency of downstream bypasses (around turbines) is seldom greater than 60 % unless natural or planned spillage coincides with the smolt run, or special guidance devices are installed and optimized at the site. Ducharme (1972) found the efficiency of a louver installation to guide Atlantic salmon smolts into a downstream bypass at Ruth Falls, N.S., varied from 57 to 80 %, depending on approach velocity and turbulence levels. Semple and McLeod (1976) found 50 % efficiency for Atlantic salmon smolts at Tusket Falls, N.S., rising to 72 % when a temporary floating screen deflector was used. Semple (1979) found 52 % efficiency for the downstream bypass at Malay Falls, N.S., with no improvement after the addition of a deflector screen.

The problem of the inundation of Atlantic salmon habitat by impoundments cannot be mitigated directly, and the only solution presently employed is fish culture (e.g., Saint John River) to replace lost natural production. The impact of long-term salmon habitat disruption by the construction of three hydroelectric dams (with fish passage devices) on the Saint John River, New Brunswick, is apparent from the angling record of the Tobique River (an upper tributary) which is depicted in Fig. 7. The combined angling record of five nearby unobstructed rivers (Jacquet, Kennebecasis, Miramichi, Nashwaak and Restigouche) are included

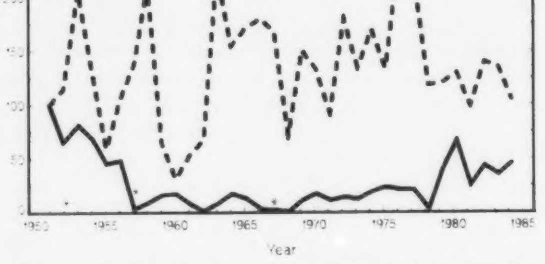


FIG. 7. Impact of dams (with fish passage) on the angling catch from Tobique River, a tributary of the Saint John River, New Brunswick. The solid line is the annual angling catch expressed as a percent of the catch in 1951, which is the initial year of the record. The three asterisks indicate years of dam construction downstream of the angling area. The dashed line is a repeat of data given in Fig. 1 for five unobstructed New Brunswick rivers, but expressed as a percent of the 1951 catch, for ease of comparison. The data sources are the same as those given for Fig. 1.

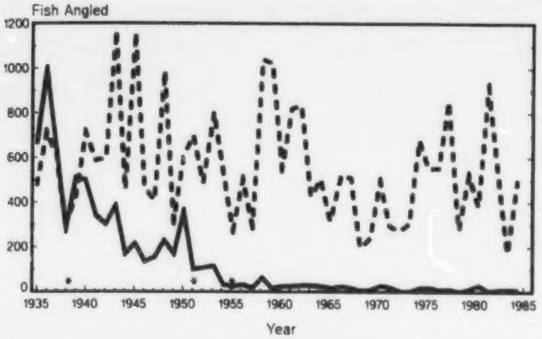


FIG. 8. Impact of dams (with fish passage) on the angling catch from Mersey River, Nova Scotia. The solid line is the annual angling catch for Mersey River. The three asterisks indicate years of dam construction (since 1955, three additional dams have been constructed without fishpassage provisions). The dashed line (included for comparison) is the annual angling catch from the adjacent Medway River, which is unobstructed. The data sources are those given for Fig. 2, and O'Neil et al. (1985).

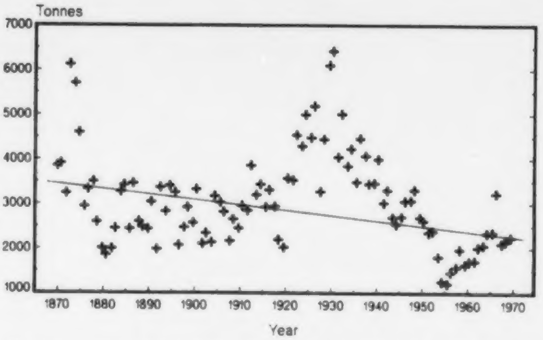


FIG. 9. Annual totals for the commercial catch of Atlantic salmon from all regions which are now a part of Canada. The downward trend (solid line) is significant to the $P<0.05$ level.

for comparison. To facilitate comparison, the data have been normalized by expressing each year's angling catch (as percent) relative to the 1951 catch which is the first year of the record. The improvement in the Tobique River angling catch, commencing about 1979, is attributable to discontinuation (in 1971) of the commercial fishery, and improvements in upstream fish passage (direct trucking of salmon to the Tobique river). Watt and Penney (1980) have shown that downstream smolt mortality has not been a serious problem on the Saint John River.

A similar disruption story, without successful mitigation, occurred on the Mersey River, Nova Scotia. The Mersey River presently has six hydroelectric dams, the first three of which were built (1935, 1951, and 1955) with fishways. Impact on the angling record is depicted in Fig. 8, where the comparison is made to the adjacent unobstructed Medway River.

Estimating Loss of Habitat Production Capacity from Catch Trends

The total annual Canadian commercial catch of Atlantic salmon since 1870 is depicted in Fig. 9. The data are taken from Dunfield, (unpubl. data) and May and Lear (1971). A regression analysis of these data indicates that by 1970 there was a significant long-term reduction of 770±260 t (24±8%) in the yield of Canada's commercial Atlantic salmon fishery ($P<0.02$). This decline of 24±8% may be looked upon as an estimate of the loss of productive capacity from Canada's Atlantic salmon habitat. This estimate may be biased by short-term events that coincidentally contribute to the long-term trend, and there may also be other long-term changes (particularly in the marine ecosystem and foreign fisheries, e.g. West Greenland) that could have some long-term impact.

The time series for total Canadian commercial catch of Atlantic salmon shows evidence of a cyclic trend with two peaks of approximately equal amplitude occurring about 1875 and about 1930. This pattern might reflect prolonged recruitment collapse following periods of chronic overfishing, or it may reflect actual changes in salmon abundance that occur in response to natural environmental cycles. A comparison of angling and commercial catches for a terminal fishery over a complete cycle would probably resolve this issue, but such data are unavailable.

The cyclic features of the times series for the total Canadian commercial catch cause a serial correlation bias in the estimation of the significance of the time trend (only the error estimate is affected, serial correlation does not contribute to the bias in the estimate of the least squares regression coefficients).

A more accurate estimate of the long-term loss of salmon habitat productive capacity can be obtained by using the Northumberland County, N.B., catch record as a no-habitat-loss control to correct for serial correlation, for changes in fishing technology and fishing patterns (e.g. the growth of the West Greenland fishery in the 1960's), and for long-term changes or cycles in the marine or freshwater ecosystems. This was done by using a variant of the multiple linear regression technique: the total Canadian catch was first regressed against the Northumberland County catch, and the residuals from this regression were then computed and, in turn, regressed against years. The long-term trend for the residuals is depicted in Fig. 10, which has been drawn to the same scale as Fig. 9 so that the reductions in error variance and serial correlation are visually apparent (the plot is actually of residual tonnes plus 3000). The residuals show a highly significant decline over the century ($P<0.01$) of 550±170 t (17±5%).

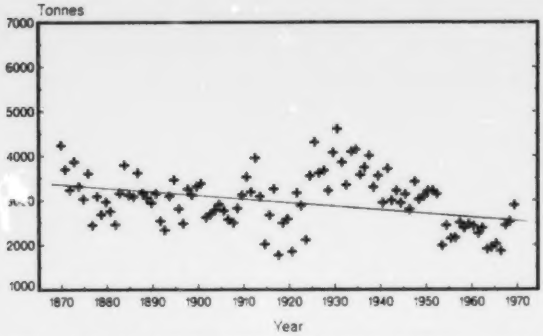


FIG. 10. Residuals (plus 3000, so that the scale is comparable to Fig. 9) from the regression of the total annual Canadian commercial catch of Atlantic salmon versus the annual commercial catch in Northumberland County, New Brunswick. the downward trend (solid line) in significant to the $P<0.01$ level. This procedure filters out most of the variation and serial correlation associated with phenomena affecting the entire (or a very large proportion) fishery. See the text for a discussion of remnant serial correlation effects.

Though considerably reduced, the serial correlation has not been entirely eliminated from the time series by the above transformation (19 df Box-Pierce test significant to $P<0.001$ level). The remaining serial correlation can be removed with an AR1 model to give a serial correlation free (Box-Pierce and Durban-Watson tests both $P>0.05$) error estimate, against which the least squares estimate of the declining trend is significant to the $P<0.005$ level. For the time series analysis, incomplete Canadian totals for the years 1895 and 1899 were estimated by interpolation to supply the missing regional values. A similar time series analysis was performed on the Northumberland County data set (the environmental control) to see how correcting for serial correlation would affect the estimated significance level of the time trend. A two parameter AR3 model removed all significant serial correlation from the error estimate. When tested against this corrected error estimate, the slope of the least squares regression on years was still not significant.

The decline of 17±5 % is a more accurate estimate of habitat productive capacity losses, but it must be looked upon as probably a minimum estimate. This is so because the Northumberland County catch, which was used as a no-habitat-loss control in deriving this estimate, is probably slightly biased by the interception (approximately 15 %) of Chaleur Bay salmon. A plausible counterargument is that there was an unusually high exploitation rate by the commercial salmon fishery of Northumberland County during the period from 1960 to 1970, thus giving spuriously high residuals for the final years of the record. If this were so, then there should be a divergence between Northumberland County catches and the remainder of the total Canadian catch. In fact, for these years, the two are unusually well correlated ($r^2=0.61$, $P<0.01$), thus negating the counterargument.

In any case, if the primary proposition of this exposition (that habitat damage is responsible for long-term impact on yield) is true, then it should be possible to account for approximately 17±5 % long-term decline in commercial salmon landings in terms of known habitat loss.

Present Status of Loss/Gain of Salmon Habitat

A balance sheet was prepared of known relative (%) salmon habitat damage and loss from 1870 to 1970, so that a comparison could be made with the long-term decline in the yield to the commercial fishery. The aboriginal habitat of the Atlantic salmon in North America, as compiled from historical records by Dunfield (1985), stretched from Long Island Sound and Lake Ontario in the south to Ungava Bay in northern Quebec. However, by about 1870, the species had largely disappeared from the New England (except for four rivers in northern Maine) and Lake Ontario portions of the range; victims of overexploitation and uncontrolled habitat destruction (especially mill dams) during the industrial revolution. Most of the New England salmon rivers were obstructed by dams early in the 19th century, and the salmon fishery in Ontario peaked in the 1850's and was reduced to a small remnant by 1870 (Dunfield 1985). The loss of these habitat areas would, thus, not be expected to impact on the total landings record since 1970, as depicted in Fig 9.

For the balance sheet, Atlantic salmon habitat was estimated simply as the accessible drainage areas of rivers, as given by the Maritime Resource Management Service (Amherst, N.S.) Table of "Watershed Areas for Nova Scotia, New Brunswick and Prince Edward Island" and by Porter et al. (1974), or else, as measured by planimeter from the 1:250,000 scale topographic map series, published by the Department of Energy, Mines and Resources, Ottawa, and the U.S. Geological Survey, Washington, D.C. Upriver limits of salmon penetration (i.e. to natural barriers) were taken from Dunfield (1985), Y. Vigneault (Dep. Fisheries and Oceans, Quebec City, Quebec, pers. comm.) and Porter et al. (1974).

The major causes of Atlantic salmon habitat destruction since 1870 are dam construction, and acidic atmospheric pollution. Watt (1986) lists thirteen former salmon rivers on Nova Scotia's Atlantic coast from which salmon have been extirpated by acidification. Also in Nova Scotia, salmon are excluded by impassable hydroelectric dams on the Nictaux, Mersey and Indian (Halifax County) rivers. In Newfoundland, hydroelectric dams and water diversion dams block fish passage on ten rivers (Porter et al., 1974), from two of which (Salmon River and Rattling Brook) the salmon populations have been eliminated (T. R. Porter, Dep.

Fisheries and Oceans, St. Johns, Nfld., pers. comm.).

Large areas of Atlantic salmon habitat have been subject to long-term damage that has reduced the productive capacity to varying extents. Watt (1986) gives a list of 18 rivers in Nova Scotia that have been acidified to the point where only small remnant salmon populations remain. Watt estimated from angling records and electroseining data that these rivers were only producing at 10 % of their pre-acidification capacity. Water diversion dams (hydropower) cause downstream habitat damage by water deprivation that reduces the amount of effective habitat, unless careful attention has been paid to the maintenance flow requirements of all life stages. In Nova Scotia, water diversions have damaged habitat on the Jordan, Ingram and Indian (Victoria County) rivers. In Newfoundland, diversion dams have resulted in reduced water levels on habitat in portions of the Grey, White Bear, Indian and Exploits rivers (Porter et al. 1974; and T. R. Porter, pers. comm.). In New Brunswick the major cause of habitat damage is the development of the Saint John River for hydroelectric power, which created a multiple fishway problem (Ruggles and Watt 1975; and Watt and Penney 1980). There is also a fish passage problem on the Petitcodiac River in New Brunswick; and the Gaspereaux and Black rivers, and East River (Sheet Harbour) in Nova Scotia have fish-passage problems as a result of a series of hydropower dams. On Quebec's North Shore there has also been some habitat damage due to construction of hydroelectric dams, most notably on the Baie de Trinite River (Y. Côté, Ministère du Loisir de la Chasse et de la Pêche, Quebec City, Quebec, pers. comm.).

Areas of agricultural damage to Atlantic salmon habitat in the Maritime Provinces have been estimated from land use maps prepared by the Maritime Resource Management Service, Amherst, N.S. The extent of agriculturally related habitat damage was checked in the field, and by reference to the Fish Habitat Data Base (Department of Fisheries and Oceans, Halifax) which contains fourteen years of Maritimes stream alteration records. No agricultural data were available for Quebec and Newfoundland, but the damage here is believed to be minimal. The data for the Maritimes indicate that most of the Atlantic salmon habitat in the Province of Prince Edward Island has been degraded by agricultural activity that has lead to extensive erosion and heavy siltation of the stream beds. Similar problems prevail in Nova Scotia, in the Annapolis Valley and Minas Basin areas (Annapolis, Kings, Hants and Colchester counties), and in the Northumberland Strait area (Colchester and Pictou counties). In New Brunswick, agriculturally related salmon habitat damage is restricted mainly to the southeast (Westmorland and Kent counties).

In addition to the salmon habitat destruction and loss that has occurred over the century, there has also been a quantity of new habitat created for the Atlantic salmon by the construction of fish passage devices around natural obstructions. In the Maritimes the major sites are the Magaguadavic River in New Brunswick, and the LaHave and Liscomb rivers in Nova Scotia. In Quebec new habitat has been opened up on the Aux Rochers and Madeleine rivers. In Newfoundland there has been an extensive program to provide Atlantic salmon access to new habitat, the largest being on the Exploits River, where a trapping and trucking facility was built at Grand Falls. Fishways have also been constructed around natural barriers on nine other Newfoundland rivers, including two built with rock-cutting techniques through natural rock outcrops on the Upper Humber River and on North West Arm Brook (Porter et al. 1974; and T. R. Porter pers. comm.).

In a geographic region as large as eastern Canada, the Atlantic salmon productive capacity of all areas of salmon habitat are not equal. Over a latitude scale from 40 to 60 degrees north, the primary control on productivity per unit area of habitat is likely to be the growth rate, which is a function of food availability and temperature. Age-of-smoltification data are available over the entire present-day North American range, and age of smoltification is a function of growth rate and water temperature (Allen 1969; and Symons 1979). Since Atlantic salmon smolts have a very uniform age, the timing of the end of the freshwater phase of the life cycle can be used as an approximate indicator of habitat productive capacity.

To relate habitat area to productive capacity, it is desirable to weight the habitat zones to allow for the differences in age of smoltification. In the Maritimes the average age of smoltification is about 2.5 yr (Elson 1962; Forsythe 1967, 1968; Symons 1979) in Newfoundland it is 3.3 yr (Chadwick 1986), in southern Labrador 4.5 yr (Power 1981), in Ungava 5.5 yr (Power 1969; and Robitaille et al. 1986) and in southern Quebec 3.4 yr (Power 1981; and Bielak and Power 1986). As a first approximation, the habitat of these five zones was weighted in inverse proportion to the average number of years required to produce a smolt; thus, the Maritimes have a habitat weighting of 1.0, Newfoundland's weighting is 0.76, southern Quebec's is 0.74, southern Labrador's is 0.56, and Ungava's is 0.45.

The final results of this compilation of relative loss and gain of Atlantic salmon habitat production potential are as follows:

A. Total loss of Atlantic salmon habitat productive capacity to chronic problems, associated primarily with agriculture, amounts to approximately 8 % (by weighted drainage area, assuming average loss in areas of habitat damage is 50 % of aboriginal productive capacity) of the total Canadian Atlantic salmon productive potential that remained at the time of Confederation.

B Habitat losses to impoundment, water diversion and obstruction (dams) amount to about 7 % (assuming 50 % loss to the next major tributary in flow reduction areas, 50 % loss above dams where fishways are provided and 100 % elsewhere) of the region's (Atlantic Canada) salmon productive potential.

C. Loss of salmon habitat to acidification has been estimated at 3 % of total Canadian Atlantic salmon productive potential (Watt 1987).

TOTAL The total loss of Atlantic salmon habitat productive potential in Atlantic Canada since 1867 is thus estimated to be approximately 18 % of the productive capacity at the time of Confederation.

D. Against this must be set the gain in Atlantic salmon habitat as a result of the construction of a variety of fish passage systems that allow upstream migrants to surmount natural obstructions. Assuming an average fish passage efficiency of 50 %, the opening of new Atlantic salmon habitat by this means accounts, up to 1970, for an increase of 2 %.

NET The net change in productive potential of salmon in Atlantic Canada since Confederation is estimated to be a loss of approximately 16 %.

Given that this balance sheet approach is subject to some rather large potential errors, it is still apparent that the estimate of loss of Canada's Atlantic salmon habitat productive potential computed from known habitat losses (and gains), is roughly the same proportion as the habitat productive capacity losses suggested by the long-term decline in yields to the Canadian Atlantic salmon commercial fishery.

Acknowledgements

I am indebted to my colleagues R. E. Cutting, C. L. Dominy, A. Ducharme, R. W. Dunfield, P. LeBlanc, L. MacGillivray, T. R. Porter, G. E. Turner, W. J. White and Y. Vigneault of the Canadian Department of Fisheries and Oceans; Y. Cote of the Quebec Ministry of Leisure, Hunting and Fishing; and Art Smith of the P.E.I. Department of Community and Cultural Affairs for their help in data compilation and in providing critical comments on the manuscript.

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Science, Inference, and the Law: The Ultimate Fish Story

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Abstract

THOMPSON, A.R., AND H. RUEGGEBERG. 1989. Science, inference, and the law: the ultimate fish story, p. 164–172. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

The purpose of this paper is to examine the use of inference in providing proof with regard to the habitat protection provisions of the federal *Fisheries Act*. The paper looks at inference in two contexts: the legal context, where inference is applied as proof of harm to fish or fish habitat in legislation and in court; and the management context, where inferences are made to derive scientifically defensible conclusions and management decisions about the risk of harm to fish and fish habitat. What are perceived to be "acceptable" levels of inference may differ in each of these contexts, and the paper suggests some of the factors that lead to these differences. However, it concludes with the notion that in either context, what is an "acceptable" level of inference is largely a policy decision rather than a scientific or technical one.

Résumé

THOMPSON, A.R., AND H. RUEGGEBERG. 1989. Science, inference, and the law: the ultimate fish story, p. 164–172. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

L'objet de ce document est d'examiner l'utilisation de l'inférence pour fournir des preuves à l'égard des dispositions concernant la protection des habitats de la Loi fédérale sur les pêcheries. On examine l'inférence dans deux contextes: le contexte juridique, où l'inférence est utilisée pour prouver que les poissons ou leurs habitats sont perturbés selon les dispositions de la Loi ou au cours d'un procès, et le contexte de la gestion, où l'on procède à des inférences afin d'établir des conclusions défendables sur le plan scientifique et de prendre des décisions au sujet des risques d'effets préjudiciables sur les poissons et leurs habitats. Une inférence « acceptable » peut différer selon le contexte, et l'on traite de certains facteurs à l'origine de ces différences. Cependant, on conclut que, dans un contexte ou l'autre, un degré d'inférence « acceptable » repose plutôt sur le jugement des décideurs que sur des données scientifiques ou techniques.

Introduction

Definition of Inference

Before beginning this examination of the use of inference in fish habitat management and the application of the *Fisheries Act*, it is important to make clear what is meant by inference. According to *Webster's Dictionary* (New 20th Century, 2nd ed.), to infer is "to conclude or decide from something known or assumed; to derive by reasoning". Inference is defined as "a deduction; a logical conclusion. [but whereas] a conclusion is full and decisive, an inference is partial and indecisive". Inference can therefore be characterized as a sequence of facts based on what is known that logically leads to a conclusion regarding the unknown.

In legal proceedings, inference plays a critical part in making proof. Every case, whether in a civil or a criminal court, involves proof of the essential facts that constitute the civil right being claimed or the crime being prosecuted. Proof is made by presenting sworn testimony, buttressed by documentary or other physical evidence or by expert opinion. In criminal cases, short of catching the accused "red handed", proof can only be presented as a logical sequence of facts from which a conclusion as to the innocence or guilt of the accused can be deduced. Therefore, inference is used by the court both to make findings of the essential facts and to reach conclusions of law.

Inference is applied in science and in management where it is impractical or impossible to carry out direct observation or tests, but where it is necessary to reach a conclusion so as to allow further formulation of scientific hypotheses or to make management decisions. In fisheries management, inferences must be used because in dealing with the complex ecological questions that fisheries management often entails, it is usually too expensive or time-consuming to directly obtain the information that is required. This is particularly true in determining cumulative effects, where inferences are drawn from what is known of site-specific or experimental effects and applied in a theoretical sense to whole systems.

Inference is applied in fisheries and habitat management in a number of ways. Extrapolation from case studies or from the historical status of the fish resource, deduction from experimental or site-specific to general situations, and induction from general principles to specific situations are all ways of inferring conclusions. For example, Mundie and Bell-Irving (1986) discuss the relative virtues of three approaches to predicting the effects of habitat change that would result from the Kemano hydroelectric proposal on salmon populations in the Nechako-Nanika River systems. These approaches are "experimental design of impact assessment, modelling changes of discharge and salmon habitat, and analysis of case histories of regulated discharge" (p.1). All are methods of inferring the impacts of that particular project on those particular salmon stocks.

The Jurisdictional Setting for Habitat Management

From experience, we know that fish are beneficial to people chiefly as food but also as integral parts of natural systems that we value. We also know that people's activities can harm fish, particularly by altering fish habitat. This experiential knowledge led the writers of the Constitution in 1867 to include a specific provision relative to fisheries — one that recognized the national character of this resource by assigning exclusive legislative power over "sea coast and inland fisheries" to the federal Parliament (s.91(12)). Parliament has set a national policy for fisheries in the *Fisheries Act*. The Department of Fisheries and Oceans (DFO) has primary responsibility for administering the Act, with a supporting role played by the Environment Protection Service of Environment Canada with respect to the administration of the deleterious substance provision of the Act.

To carry out its responsibilities, DFO is organized so as to provide a variety of management, policy development and administrative services. In executing its management policies, the department relies both on the delivery of field services (e.g., stock assessment) and on the regulation of activities that impact on fisheries (e.g., prohibitions of certain times and methods for catching fish). This latter function includes approval of activities beforehand (licensing and referral procedures) and enforcement activities after the fact (penalties and prosecutions). All of these management functions rely on a research capability to develop the scientific and technical knowledge required for the discharge of these duties. The relationships among policy, administrative activities, field services, approval, enforcement and research are shown in Fig. 1. The important thing to note is that a requirement for scientific or technical knowledge may exist at any component of the system.

Before leaving this discussion of the jurisdictional setting for habitat management, one other important factor must be acknowledged. The Constitution did not leave the provinces bereft of all legislative powers respecting fisheries. Under s.109, the provinces own fish within their boundaries as a natural resource and have legislative powers over them. Obviously then, fisheries fall into an overlapping jurisdictional field where both federal and provincial laws may be enacted. The decisive factor, however, is that in cases of conflict, federal laws prevail; hence, the provisions of the

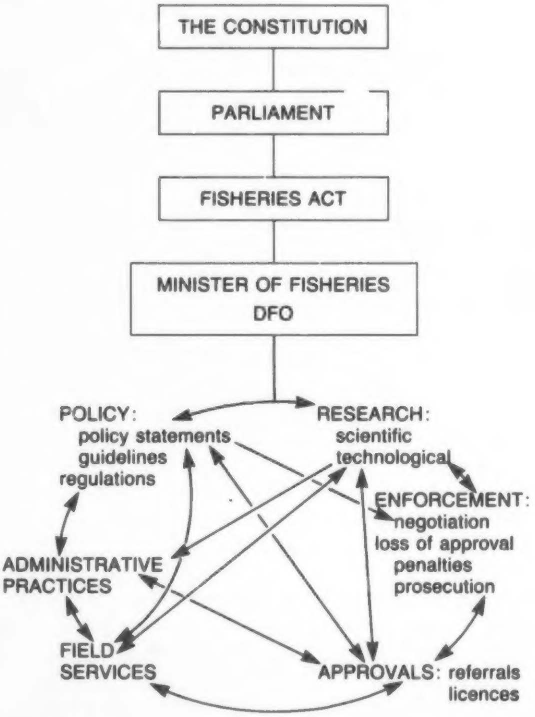

FIG. 1. Relationships in habitat management.

federal *Fisheries Act* override provincial laws to the extent there is conflict.

With regard to fish habitat, however, not only are the fish provincially owned but under the Constitution, the land and water are also owned and legislatively controlled by the provinces. Therefore, federal attempts to manage fish through the management of fish habitat can easily invade provincial legislative powers. The Canadian courts, which are responsible for interpreting the Constitution and deciding where powers lie, clearly recognize this conflicting provincial claim and feel the need to place limits on the federal fisheries power where habitat is concerned. For example, a recent decision of the Supreme Court of Canada declared s.33(3) of the *Fisheries Act*, which prohibited the putting of slash, stumps, or other debris into water frequented by fish, *ultra vires* (beyond the powers) of Parliament. Without any limiting requirement that the slash, stumps, etc. be harmful to fish, the Court ruled that this prohibition was too broad an intrusion into provincial jurisdiction to manage forest lands and logging practices (*Fowler v. the Queen* (1980) 13 DLR 3d).

As another example, Alcan recently challenged orders of the Minister of DFO with respect to the release of water from the Kenney Dam into the Nechako River in central B.C. The grounds of the challenge were twofold. First, Alcan claimed that s.20(10) of the *Fisheries Act* — which allows the Minister to order the release of water in quantities that, in his opinion, are sufficient for the safety of fish and ova — exceeds Constitutional powers with respect to fisheries in that it is an *ultra vires* invasion of provincial legislative powers to manage water resources. Second, if the court found s.20(10) to be *intra vires* (within the powers), Alcan then claimed that the Minister's exercise of the power conferred by s.20(10) was unconstitutional in this case because: (i) the Minister had allegedly failed to determine the quantity of water sufficient for the safety of fish and spawning grounds; (ii) the Minister had no adequate scientific basis for specifying the quantities of water given in the order; and (iii) the quantities of water so specified exceeded the quantities sufficient for the safety of fish and spawning grounds. The case was settled prior to trial by an agreement between the company and the federal and provincial ministers.

This case shows how the enforcement provisions of the *Fisheries Act* critically depend on scientifically defensible conclusions linking cause and effect. This warrants a closer look at the role of inference in determining legal proof in fish habitat matters.

Inference in Legal Proof

The *Fisheries Act* recognizes that management of the fisheries depends chiefly on regulation of the conduct of people who otherwise would harm fish or fish habitat. This stress on enforcement is evidenced by DFO's concentration on catch regulation and on protection of fish habitat. Prohibitions under the *Fisheries Act* or its Regulations are cast as offences punishable by criminal-type prosecution in that courts are empowered by the Act to impose severe penalties by fine or imprisonment and to issue orders in the nature of injunctions (orders to stop activities) to ensure compliance with the law.

Section 31(1) and Section 33(2)

In this scheme of things, s.31(1), which creates the offence of habitat degradation, and s.33(2), which creates the offence of introduction of deleterious substances into waters frequented by fish, are the underpinnings of DFO habitat policy and practice, both for approval and enforcement functions. Figures 2, 3, and 4 show the elements of these offences and Table 1 shows how they are defined in the *Fisheries Act*.

S.31(1) and s.33(2) affect the functioning of fisheries management by DFO in several ways. Before the fact, they set the standards by which activities and conduct will be measured. When a development project is referred to DFO for review, it is assessed by the Department as to whether fish habitat is affected, whether there will be alteration, disruption or destruction of that habitat, and whether it will be harmful to fish. As well, the project is assessed as to whether it will deposit any substances harmful to fish into waters frequented by fish. Should there be positive findings of potential harm to fish, the developer will be pressed to revise the project so as to avoid such harm. An entire program of DFO is devoted to determining appropriate responses when development projects present potential adverse effects on fish (see: DFO Policy for the Management of Fish Habitat, 1986). In the final analysis, however, all the Department can do to influence the project is to threaten prosecution for offences under s.31(1) and s.33(2) should the project proceed and offences be committed.[1]

After the fact, s.31(1) and s.33(2) prescribe the offences for which those guilty of habitat degradation

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[1] The matter is somewhat more complicated than this. Under s.33.1, the Minister could administer a formal permitting process with respect to development projects, but this power has seldom been exercised. Only in Newfoundland have regulations been established requiring developers to routinely apply for a permit to discharge wastes or alter habitat. In addition, however, regulations have been passed under s. 33(13) which set out permissible concentrations and quantities of specified substances for specific industries, such as mining and pulp mills, which new plants must meet. If plant discharges conform to these effluent standards, the owner is excused by s.33(4) from offending s.33(2) even if the discharges are in fact harmful to fish.

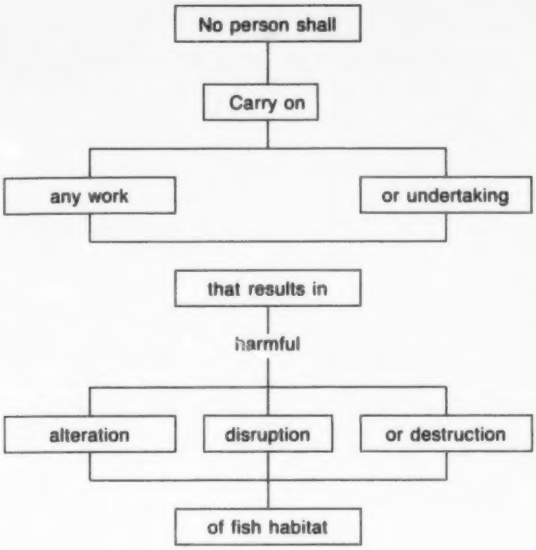
No person shall
Carry on
any work
or undertaking
that results in
harmful
alteration
disruption
or destruction
of fish habitat

FIG. 2. Analysis of s. 31(1).

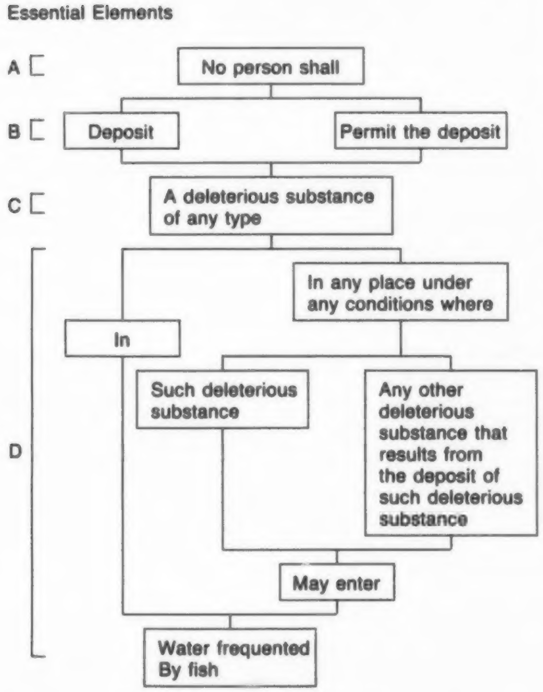
Essential Elements
A
B
C
D
No person shall
Deposit
Permit the deposit
A deleterious substance of any type
In any place under any conditions where
In
Such deleterious substance
Any other deleterious substance that results from the deposit of such deleterious substance
May enter
Water frequented By fish

FIG. 3. Analysis of s. 33(2).

or the introduction of deleterious substances can be prosecuted and, if found guilty, punished. In the case of 31(1), the prosecution must prove that (a) a person or corporation (b) carried on (c) a work or undertaking that (d) results in harmful alteration, disruption or destruction of fish habitat. In the case of s.33(2), the prosecution must prove that (a) a person or corporation (b) deposits (c) a deleterious substance in (d) water frequented by fish.

The causal connection between activity and harm to fish is often not obvious, and may require some basis in scientific knowledge that can be provided by expert evidence. As well, each element of the offence may require some conclusions of fact based on scientific knowledge. For example, in the case of s.31(1), does a work "result" in harmful alteration if the alteration occurs because of intervening natural forces some time after the work has been completed (such as a heavy rainfall causing a mud slide into a creek in a recently cleared area)?

Proof Under Common Law

In fact, given the multiplicity of circumstances surrounding potential offences against s.31(1) and s.33(2), there are many potential points of proof required. How is "proof" managed in a legal sense? Under common law, there is a well established formal framework for legal proof that is required for civil and criminal law cases. It starts with the question of onus of proof, defines standards of proof, and has rules concerning the weight of evidence. Engrafted on these common law principles are statutory rules which may shift the onus, change the standards or curtail the evidentiary requirements.

As previously mentioned, violations of s.31(1) and s.33(2) are treated as criminal offences rather than civil cases in that in their prosecution, the procedures and rules of the criminal law apply. In general, these impose much stricter burdens of proof on the prosecution because of the basic presumption of innocence in criminal cases.

(i) Onus of proof: The onus of proving a criminal case is on the prosecution. In civil cases, it rests on the plaintiff so there is no difference in this respect. What is different is the standard or burden of proof.

(ii) Standard of proof: In criminal cases the standard of proof is "beyond a reasonable doubt", whereas in civil cases, it is based on a "balance of probabilities". (By way of statistical analogy, the balance of probabilities might be likened to a 90% confidence level, whereas proof beyond a reasonable doubt might be equivalent to a 99% confidence level.) Obviously then, the burden of proving all of the elements of a s.31(1) or s.33(2) offence is extremely strict and remains on the prosecution throughout the case.

(iii) Weight of evidence: On the accused's part, evidence may be called to explain or rebut all or part of the prosecution's evidence. The judge assesses the weight of all the evidence and decides whether or not the onus of proof beyond a reasonable doubt has been met. Weight is given to evidence according to formal rules about the integrity of particular types of evidence (e.g., hearsay, documentary evidence, etc.) and also on the findings the judge makes about the credibility of those giving testimony. All in all, a good deal of judicial intuition and experience influences the judge's assessment of the weight of evidence and his decision whether or not the onus of proof beyond a reasonable doubt has been met.

Together, these principles of onus, proof beyond a reasonable doubt and weight of evidence add up to a decision that one is innocent of an offence under s.31(1) or s.33(2) unless the highest standard of proof is met. One might well wonder whether anyone would be convicted, given the strictness of proof required. In fact, the record in B.C. indicates successful prosecutions in about half the cases, with the success rate possibly declining in recent years. The total number of prosecutions, however, is quite small, and it may be that the required strictness of proof is reflected in a high degree of screening of potential offence situations, with only the flagrant ones being prosecuted.

Statutory Modifications of Proof

Be that as it may, successful prosecutions would be even fewer in number were it not for the intervention of provisions in the *Fisheries Act* that in some cases reverse the onus of proof, in others change the standard of proof to a balance of probabilities, and in still others, obviate the need for assessing the weight of evidence by deeming that certain inferences are facts.

This ability of the law to deem certain things to be true whether they in fact are or are not is a characteristic that has no counterpart in science. The criteria for its use are strictly practical and policy ones — for example, because what is deemed to be true is obviously true in most cases and time and effort should not be wasted in producing actual proof, or because actual proof would be too difficult or costly to produce and the policy of the law can be effectively served by defining away the need for actual proof.

For example, turning to the requirement of "water frequented by fish" in s.33(2), we find in s. 33(11) that the phrase is defined to mean "Canadian fisheries waters", which is then defined in s.2 to mean all waters in Canada including the fishing zones and territorial seas. By this definition, all Canadian waters are deemed to be frequented by fish. Therefore, the onus of proving that water is frequented by fish is discharged, relieving the prosecution of what would otherwise be a severe burden of proving the presence of fish in waters at the time a deleterious substance is deposited. (Note that these sections would make it impossible for the accused to establish that waters are not frequented by fish were it not for s.33.4(3) which states that water is not frequented by fish "where proof is made that at all times material to the proceeding the water is not, has not been and is not likely to be frequented by fish".)

The net result of these tortuous provisions is that the onus of proof respecting the requirement that water be frequented by fish is shifted from the prosecution to the defence. The legal inference is that all water are frequented by fish unless the accused can prove that the water into which a deleterious substance is deposited is not, has not been and will not likely be frequented by fish. Other difficult burdens of proof are eased by the Act's definitions of "fish" and "fish habitat" which include components that both enlarge the ambit of the offence and make it easier to establish proof (e.g., defining "fish" to include fish eggs(s.2) or marine plants (amend. 1985 S.C. c.31)).

Prosecutions under s.33(2) are given a further helping hand by an extensive definition of "deposit": "discharging, spraying, releasing, spilling, leaking, seeping, pouring, emitting, throwing, dumping or placing" (s.33(11)). "Deposit" is further extended by s.33.4(3)(a) which states that it "takes place whether or not any act or omission resulting in the deposit is intentional". In other words, one is inferred to be responsible for the deposit if one can be connected intentionally or not with any action or omission causing the deposit.

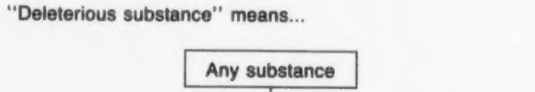
"Deleterious substance" means...
Any substance
That if added to any water would
Degrade
Alter
Or form part of a process of degradation or alteration of
The quality of that water so that
It is rendered
Or is likely to be rendered
Deleterious to
Fish
Fish habitat
The use by man of fish that frequent that water

FIG. 4. Analysis of paragraph 33 (11)(a).

TABLE 1. Terms as defined in the *Fisheries Act*.

"person"	(Note: person is defined in the Interpretation Act to include a corporation)
s. 33(8)	(8) In a prosecution for an offence under this section or section 33.4, it is sufficient proof of an offence to establish that it was committed by an employee or agent of the accused whether or not the employee or agent is identified or has been prosecuted for the offence, unless the accused establishes that the offence was committed without his knowledge or consent and that he exercised all due diligence to prevent its commission.
"deposit" 33(11)	"deposit" means any discharging, spraying, releasing,spilling, leaking, seeping, pouring, emitting, emptying, throwing, dumping or placing;
s. 33.4(3)(a)	(3) For the purpose of any proceedings for an offence under subsection (1) or section 33, (a) a "deposit" as defined in subsection 33(11) takes place whether or not any act or ommission resulting in the deposit is intentional;
"deleterious substance" s. 33(11)	"deleterious substance" means (a) any substance that, if added to water, would degrade or alter or form part of a process of degradation or alteration of the quality of that water so that it is rendered or is likely to be rendered deleterious to fish or fish habitat or to the use by man of fish that frequent that water, or (b) any water that contains a substance in such quantity or concentration, or that has been so treated, processed or changed, by heat or other means, from a natural state that it would, if added to any other water, degrade or alter or form part of a process of degradation or alteration of the quality of that water so that it is rendered or is likely to be rendered deleterious to fish or fish habitat or to the use by man of fish that frequent that water, and without limiting the generality of the foregoing includes (c) any substance or class of substances prescribed pursuant to paragraph (12) (a) (d) any water that contains any substance or class of substances in a quantity of concentration that is equal to or in excess of a quantity or concentration prescribed in respect of that substance or class of substances pursuant to paragraph (12) (b), and (e) any water that has been subjected to a treatment process or change prescribed pursuant to paragraph (12) (c);
"fish" s. 1(1) (am. 1985, c. 31)	"fish" includes (a) portions of fish, (b) shellfish, crustaceans, marine animals, marine plants and portions thereof. (c) the eggs, spawn, larvae, spat and juvenile stages of fish, shellfish, crustaceans and marine animals, and (d) such fish products and by-products as are prescribed pursuant to section 34,"
"water frequented fish" s. 33(11) s. 2	"water frequented by fish" means Canadian fisheries waters. "Canadian fisheries waters" means all waters in the fishing zones of Canada, all waters in the territorial sea of Canada and all internal waters of Canada;
s. 33.4(3)(b)	(b) no water is "water frequented by fish" as defined in subsection 33(11) where proof if made that all times material to the proceedings and the water is not, has not been and is not likely to be frequented in fact by fish.
"fish habitat" s. 31(5)	(5) For the purposes of this section and sections 33, 33.1 and 33.2, "fish habitat" means spawning grounds and nursery, rearing, food supply and migration areas on which fish depend directly or indirectly in order to carry out their life processes.

Finally, the term "deleterious substance" is given an extended definition under s.33(11) which requires a causal connection between deposit of the substance and harm to fish, but says that potential harm is sufficient. The waters need only be "rendered" or "likely to be rendered" harmful to fish; i.e., it is not necessary that the substance actually make those particular waters harmful to fish, but simply that *if the substance were added to water*, it would likely render the water harmful to fish. Courts in British Columbia have construed this definition to mean that the gist of the offence is the harmful nature of the substance rather than the state of the receiving water after the addition of the substance (*Regina v. MacMillanBloedel Ltd* (1979) 47 C.C.C.(2d)118): "once it is determined that (the substance in question) is a deleterious substance and that it has been deposited, the offence is complete without ascertaining whether the water itself was thereby rendered deleterious".

By this interpretation, the fact that there may be no actual harm to fish or fish habitat (e.g., because of dilution) is no longer a key factor. The offence is complete because harm to fish or habitat is inferred from the mere fact that a harmful substance has been deposited. This means that the crux of the prosecution's case is proof that the deposited substance is itself harmful to fish. Case law in B.C. shows that this onus can be met by expert evidence based on a standardized LC-50 test.[2]

In this way, in B.C., the very difficult onus of proving that the receiving water body is made harmful to fish or fish habitat is avoided[3]. In a sense, the section accomplishes a reversal of onus respecting this element of proof. An accused would certainly be acquitted if he/she could prove that a deposit has caused no harm to fish or fish habitat, but this onus is as difficult to meet as the onus of proving the contrary.

Summing up with respect to s.33(2), the offence is so constructed as to make conclusive inferences against accused persons respecting what constitutes "fish" and "fish habitat", what waters are "frequented by fish", what are "deleterious substances", and what amounts to a "deposit". The result is that the prosecution must prove its case beyond a reasonable doubt, but it will strike home under s.33(2) merely by proving a deleterious substance has been deposited in water.

It is important to point out that a form of defence known as the "due diligence defence" operates under s.33(8) to restore the balance in favour of individual freedom of action to some degree. This subsection provides that the accused may raise a defence that he/she exercised all due diligence to prevent the commission of an offence. The onus of proving due diligence rests on the accused, but the standard is not proof beyond a reasonable doubt. Rather, the accused may prove on a balance of probabilities that there was no want of care in attempting to avoid the offending action, and be acquitted on that basis.

Conclusions Regarding Inferences in Legal Proof

The omnipotence of the law is made apparent! Should questions about inferences in legal proof stand in the way of achieving what Parliament considers to be a right or just balance between freedom of human action and harm to fish, Parliament can legislate them away. It has done so in the the *Fisheries Act*, obviously seeking to create offences in relation to complex biological systems that can be successfully enforced despite scientific uncertainties or logistic impossibilities.

Acceptance of Inference

The previous section makes it clear that in the legal context, the way in which several important provisions of the *Fisheries Act* are worded greatly reduces the need to defend the use of inferences regarding some aspects of fish habitat matters. In essence, these provisions deem certain inferences regarding attributes of fish habitat to be accepted as facts under the law. Probably, many more inferences could be obviated by further "manipulation" of the legislation.

Inference in the Management Context

Despite statutory modifications that ordain some inferences as sufficient legal proof, there still remain innumerable circumstances in the legal context where a scientifically valid basis for proof is required if an offence regarding fish habitat is to be successfully prosecuted. The same holds true for the many other situations in which habitat managers and scientists are involved:

i) making "field" management decisions, including responses to referrals from other government agencies, negotiations with private interests over avoidance or mitigative measures, and taking regulatory actions.
ii) establishing guidelines and regulations.
iii) presenting information and opinions at informal or quasi-judicial hearings; e.g., the West Coast Offshore Exploration Environmental Assessment.

In these contexts, managers and scientists rely heavily on inferences to reach conclusions about the risk of harm to habitat resources.

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[2] The generally accepted procedure involves the use of samples collected at the site of deposition into water. Conditions in the laboratory should approximate the environmental conditions; e.g., ambient water temperature, oxygen content, etc. The test species of fish (a species likely to be found in the waters in question) is introduced into the sample and mortality is measured over a 96-hour period. Mortality in excess of 50% is normally considered proof that the sample is a "deleterious substance".

[3] In Alberta, the courts have taken a stricter view, requiring that the prosecution prove that the receiving waters themselves are made harmful to fish. This difference in interpretation of the Act between B.C. and Alberta courts will likely one day be resolved by the Supreme Court of Canada.

An Illustration: the CN Twin Tracking Project

Such circumstances where inference plays a crucial role is illustrated by the Canadian National Railway (CN) twin-tracking project along the Thompson–Fraser River corridor in B.C. To complete its second track, CN proposed to dump rock fill on the river side of its existing track so as to form a widened road bed. This rock would in many places fill in the river's edge, changing the configuration of the shoreline. Two significant questions about potential harm to fish have arisen as a result:

i) would the rock displace natural resting and rearing habitat to a significant extent by reason of the fact the natural sinuousities of the shoreline would in many places become a wall of rock? and would this result in a decline in the reproductive success of salmon stocks in the rivers?

ii) would the wall effect so alter current flows in the river as to place increased demands on the energy budget of migrating salmon, also resulting in some overall loss of spawning success in the upper reaches of the rivers?

As to the legal answers to these questions, it is quite certain that CN would alter and in some cases destroy fish habitat, and would definitely be depositing a substance into waters frequented by fish. The issue rather depends on proving harm to fish: under s.31(1), whether the alteration would be harmful to fish habitat and under s.33(2), whether the substance deposited would be deleterious to fish, fish habitat or the use of fish by man. If the issue was ever to be taken to court, these would have to be proved beyond a reasonable doubt. In that case, a defence might attempt to show that the alteration merely displaced fish to other locations along the river where resting or rearing could occur (assuming the other locations were underutilized), and therefore was not harmful. As to whether rock placed in water is itself a deleterious substance, this burden of proof could not be easily met except where rock has been deposited directly on spawning grounds.

As to the effect of increased current flow on fish, there are many difficulties in proving harm beyond a reasonable doubt. It is not the individual instances of alteration or of depositing rock that is in question but rather the *cumulative* effect that can cause harm to fish. Theoretical models have been developed to simulate the changes to the riverbed and constriction of the river as a result of construction in an effort to predict increases in flow. Likewise, there are probably theoretical models addressing the question of whether increases in flow lead to stress to fish. However, scientifically proving that the flow increases will be harmful to fish, not just in a theoretical sense but in the sense of proof of harm beyond a reasonable doubt, is highly speculative.

What does this mean for fish scientists and managers? If the problem is serious enough — e.g., a threshold judgement must be made in a court situation — a major concentration of research effort would be required to provide quantitative data that conclusively link the placement of rock to increased current rates which in turn cause higher energy budgets and reduced spawning success in fish. This task could be insurmountable. Alternatively, managers could try to persuade their political masters to introduce amendments to the *Fisheries Act* to the effect that a substance deposited in water that increases the rate of flow of water through fish habitat is deemed to be a "deleterious substance". In this way, the question of what is an acceptable degree of inference can be bypassed.

What is more likely is that DFO managers will use their resources of logic and persuasion to deal with the question at a management rather than legal level by attempting, with the proponent, to find acceptable means of avoiding or minimizing the perceived impacts. In this management context, the challenges to inferential knowledge are typically less rigorous and the acceptable level of inference more lenient, than in the courtroom context. In the CN situation, for example, a Technical Working Group of federal, provincial and CN representatives was established to address the many scientific and technical uncertainties that were involved. A variety of experiments and modelling exercises was initiated to establish the logical sequence of facts and inferences that would make the general, intuitive conclusion that dumping rock will ultimately harm fish acceptable to all parties.

One might suggest, therefore, that "acceptable" levels of inference in the management context are determined as the situation unfolds. A project proponent will likely accept more "liberal" (less rigorously developed) inferences regarding harm to fish when negotiating terms and conditions of project activities than if the issue of impact to fish escalates to court proceedings. The same can be said of the acceptance of the proponent's inferences by government scientists and managers.

Factors Influencing the Acceptance of Inference

Probably the most critical role of habitat management is assessing and quantifying risks to the resource resulting from a particular action. In any such assessment, scientists, managers and other interested parties may differ among themselves over what are acceptable degrees of inference for a variety of reasons. Some of these might be called "objective" factors:

— the various parties may base their judgment on different information or different interpretations of the "facts" leading to the inference;

- they may differ in their level of confidence in these facts;
- they may be using different models of the relationships within natural systems from which inferences are derived; or
- they may disagree on the methods or formulae used in establishing probabilities of harm.

Other factors are best described as "subjective" or "normative":

- the parties may be judging the issue at hand in relation to different objectives, stakes and values;
- they may differ in their perceptions of the types and magnitude of risks involved;
- they may have different risk propensities, meaning that even if they are faced with the same probability distribution describing the likelihood of harm, one group would say that the action is too risky and another would say it is "safe"; or
- they may differ in their willingness to make tradeoffs between resource uses.

The *Fisheries Act* obliges DFO to assess risks. For example, s.20(10) provides the Minister with the power to issue orders regarding the release of water from dams and other obstructions that are "sufficient for the safety of fish and for the flooding of spawning grounds to such depth as will, in the opinion of the Minister, be necessary for the safety of the ova deposited thereon". This discretionary authority necessitates two decision-making processes on the part of the Minister: (i) to analyze and predict the probabilities of harm associated with alternative outcomes of a given action that may impact negatively on the habitat resource; and (2) to assess the acceptability of each of these probabilities from the standpoint of his/her mandate to provide for the "safety" of fish and spawning grounds. The first is largely a scientific or objective process, the second a political or normative one. Both processes involve the use of inferences; the first in applying scientifically-derived information to predict unknown outcomes, and the second in determining society's standards of acceptable risk to the resource.

The Scientists' Role

In theory, the role of the scientist or technician in these situations is to give an informed opinion in assessing the probability and severity of harm to fish. Accordingly, differences in opinion between scientists should lie in the methods that are applied, the data that are used or the inferences that are drawn in measuring this probability. Scientific assertions or debates should not, in theory, be influenced by the scientists' values or stakes in the issue, or by their own propensity to take risks or make trade-offs. In practice, however, it is often suspected that these factors do influence scientists' opinions.

Nonetheless, while scientists are expected to play an objective role in risk prediction, this process often relies heavily on the use of inferential knowledge — and herein lies a dilemma. While the scientist may not be explicitly stating it, his/her opinion of acceptable risks may be colouring his/her acceptance of pertinent inferences in the prediction process. Is it possible to determine "acceptable" degrees of inference on a purely objective basis when these inferences are ultimately being used to judge "acceptable" levels of risk? If so, where are these objective sources? The *Fisheries Act* is not much help. For instance, it does not state whether "safe" as it is applied in s.20(10) means absolutely free from risk or a 20 % chance of killing half of a given fish stock. In fact, most legal and policy analysts interpret the Act as being risk averse so far as harm to fish are concerned, and that DFO's mandate is to avoid risks to habitat at all costs. This has led to DFO's reputation of failing to recognize the values associated with other resource uses and its unwillingness to make tradoffs between fish habitat and these other uses.

The Role of the Political Arena

Obviously, acceptable levels of risk to fish habitat are ultimately determined in the political arena. The development and interpretation of laws and management policies are subject to the attitudes of the society in which they are created and applied. It follows, then, that inferences used to determine the probability of harm will be judged in this political context. Society's support for more or less strict interpretations of the *Fisheries Act*, and with it more or less stringent use of inferential knowledge in fisheries management, will certainly be influenced by improvements in our scientific understanding of fisheries systems. But the acceptance of inferences regarding habitat resources will also be dictated by the sympathies of society towards protecting these resources in the face of other values and development pressures.

Perhaps the ultimate fish story is that however much we may wish to pursue scientifically sound fisheries management strategies, the reality is that social policies and values will continue to dominate the outcomes of management decisions. So far as the *Fisheries Act* is concerned, the public may demand strict offences and harsh penalties; prosecutions will continue to require proof beyond a reasonable doubt; science and inference will continue to fall short of the standard of proof; and hence, legislatures will continue to bypass scientific limitations by deeming necessary inferences to be true.

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Habitat Models and their Predictive Capability to Infer Habitat Effects on Stock Size

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Abstract

SHIRVELL, C. S. 1989. Habitat models and their predictive capability to infer habitat effects on stock size, p. 173–179. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Fisheries scientists expect that habitat models will identify important habitat variables, describe how ecosystems work, and predict positive or negative relationships between fish populations and habitat parameters. Habitat models are often intended to be spatially transferable so that their predictions are useful for populations or environments other than those from which they were derived. Six mathematical models of the relationship between fish populations and their habitat were reviewed to assess how well these expectations were met. Out of a total of 33 possible variables considered by all six models, no variables having significant correlations with fish abundance were common to all six models. Water depth was the variable most frequently correlated with fish abundance and had significant correlations in four of the models. The optimum level of any single habitat variable for a species was relatively constant between geographic areas but the importance of any habitat variable relative to any other was not constant between geographic areas. Models were therefore valid only for the geographical region where they were developed but results can not be extrapolated to new situations without recalibration. For the data sets from which they were derived, these models explained 50–96 % of the variation in fish numbers or biomass (mean = 76 %). For data sets from which they were not derived, they explained 7–30 % of the variation in fish numbers or biomass (mean = 24 %). Calibrated habitat models can predict quite well for the data sets from which they were developed but they will not prevent management decisions which result in undesirable ecological consequences unless their appropriateness is confirmed before each application.

Résumé

SHIRVELL, C. S. 1989. Habitat models and their predictive capability to infer habitat effects on stock size, p. 173–179. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Les scientifiques spécialisés dans le domaine des pêches prévoient que les modèles d'habitats permettront de déceler les variables qui revêtent de l'importance dans ceux-ci, de décrire le fonctionnement des écosystèmes et de prédire les relations positives ou négatives qui existent entre les populations de poissons et les paramètres des habitats. Dans bon nombre de cas, les modèles d'habitats sont destinés à être transférables dans l'espace de sorte que leurs prévisions puissent être utiles pour des populations ou des environnements qui diffèrent de ceux sur lesquels ils reposent. On a examiné six modèles mathématiques des rapports entre les populations de poissons et leurs habitats afin de déterminer dans quelle mesure ils satisfaisaient aux attentes. Sur un total de 33 variables possibles considérées par les six modèles, aucune variable présentant des corrélations significatives avec l'abondance des poissons n'a été retenue par tous les modèles. La profondeur de l'eau était la variable qui a été le plus fréquemment mise en corrélation avec l'abondance des poissons, et des corrélations significatives à cet égard ont été obtenues avec quatre modèles. La valeur optimale de toute variable particulière d'un habitat pour une espèce donnée était relativement constante d'une région géographique à l'autre, mais l'importance d'une variable donnée par rapport à toute autre ne l'était pas. En conséquence, les modèles n'étaient valables que pour les régions géographiques auxquelles ils étaient destinés au départ, et les résultats ne peuvent être appliqués par extrapolation à de nouvelles zones sans procéder au préalable à un réétalonnage. Dans les séries de données pour lesquelles ils ont été élaborés, ces modèles expliquaient entre 50 et

96 % de la variation des effectifs ou de la biomasse des poissons (moyenne de 76 %). En ce qui concerne les séries de données auxquelles les modèles ont été appliqués par la suite, ceux-ci expliquaient entre 7 et 30 % de la variation des effectifs ou de la biomasse des poissons (moyenne de 24 %). Les modèles d'habitats étalonnés peuvent donner des prévisions assez bonnes quant aux séries de données auxquelles ils étaient destinés au départ, mais ils ne peuvent prévenir des prises de décision qui se traduiront par des conséquences écologiques nuisibles à moins de veiller à ce qu'ils se prêtent aux zones étudiées avant chaque application.

Introduction

Habitat models are becoming more commonly used in fisheries research and management to solve problems. Common uses of ecological models are (1) to explain the functioning of ecosystems, (2) to predict sizes of populations, (3) to generate hypotheses about the environment or population for investigation, or (4) to serve as reference points against which observed levels of ecological process can be compared (Pielou 1981). Examples of these generalized purposes restated as fisheries goals would be: to identify important (= limiting?) habitat variables, to measure habitat change, to determine the suitability of habitat for outplanting hatchery production, to achieve no-net-loss of productive habitat capacity, or to manage stocks by predicting biomass yield and appropriate exploitation.

The use of habitat models can present problems. However, the popularity of habitat models may be creating unrealistic expectations for their ability to solve fisheries problems. Failure to recognize a model's inherent limitations may result in it being used in geographic locations or for fish communities where its use is unwarranted. Blind faith in habitat model predictions which are incorrect could result in mismanagement of fish stocks or their habitat.

The objectives for this review of habitat models were to identify the intended purposes of habitat models, summarize the predictive performance of some common habitat models, and assess the utility of habitat models generally in meeting fisheries science expectations.

The Models

Habitat models are based on a functional relationship assumed to exist between the fish population and its environment. That is, by measuring selected habitat attributes it is assumed to be possible to predict the size of fish populations likely to occur there.

A generalized habitat model might be thought of as follows:

$$\text{(1) Fish abundance or biomass} = a\,(\text{habitat variable } 1)^{b} + c\,(\text{habitat variable } 2)^{d} + \ldots\, x\,(\text{habitat variable } i)^{y}$$

where "habitat variables" are various environmental features thought to affect fish distribution or metabolism, and a, b, c, d, x, and y are appropriate weighting coefficients. This is a classic multiple regression equation where the performance of the model, the important habitat variables in it, and the interactions between the variables are all assessed using the amount of variation in the fish population's abundance or biomass "explained" by the equation.

I reviewed the performance of six freshwater habitat models published in the literature during the last two decades (Table 1). All of these models are regression analyses similar to equation (1) and have been used to predict the standing crop of fish populations (or some other index of the population's size, in some cases catch or yield) from measurement of the population's environment. The six models all share one of two common purposes: models 1, 4, and 5 (Table 1) were developed to predict the size of the fish population from physical attributes of the environment, and models 2, 3, and 6 were developed to identify limiting habitat factors and a way of combining them so that the derived index would correlate with the standing stock of the fish population. The Physical Habitat Simulation model (Stalnaker 1979) is somewhat different from the others in that it is most commonly used to predict the amount of "fish habitat". Stalnaker (1979), however, calculated a 1:4.5 relationship between fish "habitat" and fish biomass, and implied that habitat quantity calculated from PHABSIM can be used to predict the biomass of fish in certain Wyoming streams. The criteria I used for assessing how well the habitat models achieved their intended purposes were the coefficient of determination (r^2 = of the regression analyses and the level of significance of the correlation coefficients between the fish population and individual habitat variables in the models.

The models selected for review have had widely varying application and testing. Five of the models (numbers 2–6, Table 1) were developed for rivers and streams; the first model was developed for lakes. There are a few regression models using abiotic variables for the estuarine or marine environments (e.g. Schweigert and Fournier 1982; Hay and Kronlund 1987; Blackbourn 1987) but they were not included in this review.

The Morphoedaphic Index (Ryder 1965) and the Physical Habitat Simulation Model (PHABSIM, Stalnaker 1979) while originally developed for restricted geographic locations have possibly had the widest geographic application while Milner et al.'s 1985 model

TABLE 1. Common habitat models used to predict fish biomass or abundance.

Model	Reference	Year	Geographic area model was originally developed or applied[a]	Number of habitat variables	% variation explained for data sets models were derived from	% variation explained for data sets models were not derived from
1. Morphoedaphic Index	Ryder	1965	34 Canadian lakes 210 south USA reservoirs 7 central African lakes 46 lakes in Finland	2	75 % lakes 62 % reservoirs	11 %[c]
2. Physical Habitat Simulation (PHABSIM)	Stalnaker	1979	8 Wyoming streams	3	80 %	0–<50 %[d]
3. Habitat Quality Index (HQI)	Binns and Eiserman	1979	36 Wyoming streams	11 (9 sig)[b]	96 %	7 %[e]
4. Milner et al.	Milner et al.	1985	8 rivers in Wales	13 (8 sig)	93 %	50 %[f]
5. Habitat Evaluation Procedures (HEP)	Layher and Maughan	1985	16 streams in Kansas and Oklahoma	19 (10 sig)	50 %	27 %[g]
6. Bowlby and Roff	Bowlby and Roff	1986	20 streams in southern Ontario	33 (6 sig)	62 %	not tested elsewhere
					$\bar{X} = 76\%$	$\bar{X} = 24\%$

[a] Geographic location from reference cited.
[b] The number of variables that had significant relationships with fish biomass or abundance.
Reference for the models tested in new applications.
[c] Jenkins (1967).
[d] Scott and Shirvell (1987).
[e] Bowlby and Roff (1986).
[f] Milner et al. (1985).
[g] Layher and Maughan (1985).

and Bowlby and Roff's 1986 model the narrowest (Table 1). The Habitat Quality Index (HQI, Binns and Eiserman 1979) and the Habitat Evaluation Procedures (HEP, Layher and Maughan 1985) so far have had intermediate application. All six models were originally developed for salmonids or other cold-water fish species although some of the models have been subsequently applied to habitats of warmwater species (e.g., Jenkins 1967; Regier et al. 1971; Layher and Maughan 1985), birds (Lumsden 1984), snakes (Ken Bovee, 2625 Redwing Rd., Fort Collins, CO 80526, personal communication), and even Loch Ness Monsters (Sheldon and Kerr 1972).

The Habitat Variables

Many variables have been speculated to influence the size or production of fish populations (Table 2). Using stepwise multiple regression analysis, inclusion and deletion of various habitat variables have been tested in the models to determine the effect on the overall model performance (percent of population variation explained). The exception to this is the Morphoedaphic Index and PHABSIM where it is implicity assumed that the variables they include are important, but that if the models' predictions do not show a statistically significant relationship with the fish population, then the variables in the two models are not acting as limiting factors for those populations being considered.

Of the 40 variables commonly hypothesized as potentially determining fish population size, only 15 were found by the six models to have significant correlations with the fish population (Table 2). In all six models then, the habitat variables actually limiting the fish populations were some smaller subset of the total number of variables initially considered.

Only two of the models (Habitat Quality Index, Binns and Eiserman 1979, and the Bowlby and Roff 1986 model) considered biotic variables (food or predators) as possibly having importance while the other four models considered only abiotic (physical habitat) variables. All of the models except PHABSIM included some variable related to metabolic production (water temperature or some water chemistry index of productivity like total hardness).

I compared habitat variables of the six models to

TABLE 2. Habitat variables used by habitat models to predict fish abundance or biomass (adapted from Milner et al. 1985).

A. CATCHMENT ATTRIBUTES (8 significant variables)

Geomorphological Features	Hydrological Features	Water Chemistry Features
1 *Altitude*	9 Average daily flow	16 pH
2 Geology	10 Average seasonal flow	17 *Hardness TDS*
3 Catchment area	11 Flow pattern	18 Alkalinity
4 Total channel length	12 *Extreme flow variations*	19 *Nitrogen (NO_2)*
5 Drainage density	13 Stability of flow	20 Phosphorous
6 Mean basin length	14 Precipitation	21 Dissolved solids
7 Mean basin slope	15 *Water yield*	22 Conductivity
8 Forest ratio		23 *Temperature*
		24 *Turbidity*
		25 *Oxygen*

B. SITE ATTRIBUTES (7 significant variables)

26 *Width*
27 *Depth*
28 *Substrate composition*
29 *Instream cover* — debris, rocks, macrophytes
30 *Bankside cover* — undercut banks, log jams
31 Sinuosity
32 *Bank erosion*
33 Water surface area
34 Volume
35 Flow type
36 Riffle: pool ratio
37 *Velocity*
38 Gradient
39 *Fish food abundance*
40 *Fish food diversity*

NOTE: Habitat variables in italics had mathematically significant correlations with fish biomass or abundance.

determine which, if any, of the significant habitat variables were common to all six models. None were. Of the 15 habitat variables found by one or more of the models to have significant correlations with the fish population, the variable most frequently important was water depth which was significant in four of the models. Next most frequently significant were water velocity, substrate, cover, width, and total dissolved solids which were significant in three of the six models, fish food abundance or diversity, water temperature, and turbidity were significant in two of the models, and annual streamflow variation, bank erosion, nitrogen (NO_2), water yield, dissolved oxygen, and altitude had significance in only one of the habitat models.

Clearly, no single habitat variable or group of variables was universally regulating fish production; different populations were limited by different characteristics of the environment. However, for most of the populations to which these habitat models have been applied, the levels of the various habitat variables experienced would have been within the species' tolerable range. Only when the levels of habitat variables exceed the species' preferred levels might distinct correlations with fish biomass be detectable, at least with the sampling intensity normally used in field investigations. As a consequence, the determination of whether a habitat variable in Table 2 is important or not may be an artifact of the models or the specific studies of those models that I included in my review.

A second problem of identifying important habitat variables from regression analysis is that variables can be interrelated (i.e. colinear). Collinearity can result in confusion of which habitat variables are important because their influence on the fish population is blurred together in the regression model. This problem is most common when many habitat variables are considered together in a regression model but it can be important even when only a few variables are considered if a polynomial regression model is used. PHABSIM, which uses only three variables (Table 1), is an example where interaction between the variables can sometimes explain more of the variation in fish biomass than any of the habitat variables individually (Orth and Maughan 1982, their table 3). Ryder et al. (1974) describe how frequent partial correlations between variables originally considered for the Morphoedaphic Index cause the single variables of total dissolved solids and mean depth to effectively represent many interrelationships with the ecosystem. Consequently, variables determined to be important by regression analysis may be acting as surrogates for other aspects of the environment.

The Predictive Capability of the Models

The mean variation in fish biomass explained by the six habitat models was 76 % (Table 1). Because this was for populations and environments from which the models were developed or calibrated, this level of "explanation" should be regarded as the best performance which could be expected of the models.

Even for those situations when habitat models have the best fit to the empirical data, 4–50 % of the variation in fish biomass or abundance was unexplained by the condition of the habitat. This unexplained variation may simply be due to error in the measurement of either the fish population or the habitat variables. Another explanation may be that other habitat variables not considered, or other factors such as fishing exploitation may be causing the unexplained variation.

As an example of exploitation accounting for the unexplained variation, Stalnaker (1979) specifically excludes two populations from his analysis due to the influence of fishing he expected had occurred on the observed standing crops, while Bowlby and Roff (1986) also comment on the possibility that exploitation could be the cause of the unexplained variation, but argue that it was not. Exploitation could reduce the standing stock of resident fishes or recruitment to the freshwater phase of anadromous fishes in such a way that the observed biomass of the population may be under the carrying capacity of the habitat it is observed to be occupying. Theoretically, the inference from habitat regression models is that all remaining unexplained variation in the fish population was due to fishing. However, that would be unlikely. Nevertheless this possibility demonstrates the danger of hasty inferences about the environment drawn from measurements of fish population abundance.

Although the habitat models explained the majority of the variation in fish populations for the data sets they were developed from, the amount of variation explained was much less when the models were applied to "new" geographical locations (Table 1). This is not apparently due to any shift in the habitat preference or physiological performance of a species in different geographical areas. Shirvell and Dungey (1983), Layher and Maughan (1985), and Morantz et al. (1987) have all shown that single species of fish demonstrate preference for similar levels of the same physical variables in several different environments. Moreover, the levels of individual habitat variables where the best physiological performance occurs is approximately similar throughout a species range (see Alderdice 1972 for a discussion). By inference then, the failure of these habitat models to perform well in "new" geographic areas indicates that the same habitat variables are not acting as limiting factors to the same extent in all environments within the species' range. This is confirmed by Layher and Maughan (1985) and Bowlby and Roff (1986) because they were able to greatly increase the amount of "explained" variation in the fish population by building new habitat models using *different* habitat variables.

Because different habitat variables limit different fish populations, habitat models may not be widely transferable. Users seem to incorrectly assume that habitat models are "species-specific" and apply them to new environments where the same species that the models were originally developed for are present. In fact, it appears the models are "location or environment-specific". This, unfortunately, defeats the intended purpose of "efficient explanation". Because it is impossible to investigate every population or environment, habitat models have often been turned to as techniques for efficiently gathering knowledge about large geographic areas. This reliance is based on the assumption that results from a small number of localized lakes or streams are representative of the responses to be expected from a much larger number of lakes or streams over a larger area. The failure of habitat models to make accurate predictions in new applications defeats this purpose.

Evaluation of Habitat Models

How well habitat models meet their intended purposes is a function of the way they are developed and the implicit assumptions that lead to that form of development. The habitat models in Table 1 fall into two groups based upon implicit assumptions they incorporate about the habitat variables. The Morphoedaphic Index and PHABSIM use habitat variables which are *a priori* assumed to be important, while the other four models make no presupposed assumptions of their importance. Different variables are tried in turn until the best combination is found.

This difference in model development results in the two types of models better meeting different purposes. Obviously models which incorporate *a priori* variable assumptions prevent those models from identifying new important habitat variables limiting specific populations, while those models with no variable preselection identify the best or most important habitat variables in each situation. On the other hand, the Morphoedaphic Index and PHABSIM retain the purpose of efficiency and wide application while giving up predictive precision. The usefulness of their predictions diminishes to irrelevance in environments where habitat variables other than the ones they use are limiting the population.

The other models, which are "custom-fit" to the data they are developed from, give up the purpose of wide application in an attempt for greater predictive precision.

The predictive capability of habitat models may now be at its maximum. Models like the Habitat Quality Index (Binns and Eiserman 1979) which have unconstrained variable inclusion and incorporate biotic variables like food availability, predators, or competition, and metabolically related variables like water temperature and total dissolved solids now produce predictions which explain better than 90 % of the variation in fish biomass. However, even when most of the variation has been accounted for caution is required when drawing inferences from the model. Numbers and formulae delude users into thinking that a phenomenon has been "explained". However, the cause and effect relationship is rarely as direct as is implied by the model. Accurate predictions based on observations or data from the present and past are possible only when the environment under observation is stable, isolated, and highly recurrent. Because most freshwater ecosystems lack these characteristics there may be no advantage gained by attempting to increase the current precision. "... the futility of striving for an exact match between models and reality" (Pielou 1981) may be both an unrealistic expectation and goal for habitat models. At best models will always be some simple approximation of reality.

Failure to achieve perfect prediction does not eliminate the usefulness of habitat models to fisheries science, however. "It is not the resemblance between models and reality that lead to new discoveries, but the discrepancies between them" (Pielou 1981). Failure by models to explain or predict ecosystems can generate new hypotheses about ecosystem processes and environmental variables. Habitat models can also confine thought, however, especially when they are routinely applied to "solve" fish or habitat management problems. Models that utilize preconceived assumptions about which habitat variables are important, for example, eliminate investigation about the role of other variables.

Because the same habitat variable is not limiting all populations, habitat models cannot routinely be transferred to new situations without recalibration or verification. New studies are required to test the truth of assumptions implicity embodied in the models especially when the models are used for predicting future states of the environment or to infer the population's response. While such testing normally occurs during model development (the research phase), the need for such studies is frequently overlooked in model application where the assumptions are accepted as valid because they are intuitive.

Acknowledgments

I am grateful to colleagues everywhere who have challenged my ideas on models and by so doing have helped advance techniques we need to solve fisheries problems. I would like to thank Drs J.N. Bowlby, R.A. Ryder, and an anonymous reviewer for helpful comments which improved the presentation of these ideas.

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The Adaptive Significance of Marginal Populations: A General Perspective

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Abstract

SCUDDER, G. G. E. 1989. The adaptive significance of marginal populations: a general perspective, p. 180–185. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

Populations of a species normally undergo successive expansions into less favourable, "hard", marginal habitats, alternating with contractions into more favourable, central "soft" refuges. These expansions and contractions are the inevitable consequences of density fluctuations. The "hard", ecologically marginal habitats are characteristically spatially diverse and temporarily unstable. Selection in these is for colonization ability and adaptation to a diverse array of density-independent factors. Centripetal gene flow from these marginal areas at times of contraction increases the genetic diversity of the central population, wherein selection usually favours density-dependent factors. Thus, central genetic diversity is enhanced and enriched. Studies of diverse organisms show that the greatest genetic diversity is found in the most ecologically versatile species. Marginal populations have a high adaptive significance to the species as a whole, and marginal habitat conservation, preservation and management is one of the "best" ways to conserve the genetic diversity and resources of fish species. Marginal habitats are an essential prerequisite for the maintenance of this diversity and versatility.

Résumé

SCUDDER, G. G. E. 1989. The adaptive significance of marginal populations: a general perspective, p. 180–185. *In* C. D. Levings, L. B. Holtby, and M. A. Henderson [ed.] Proceedings of the National Workshop on Effects of Habitat Alteration on Salmonid Stocks. Can. Spec. Publ. Fish. Aquat. Sci. 105.

En règle générale, les populations d'une espèce gagnent, tour à tour, des habitats marginaux moins favorables où ils s'étendent, puis des refuges centraux où ils se concentrent en petits groupes. Ces phénomènes d'extension et de concentration sont les conséquences inévitables des fluctuations de la densité des populations. Les habitats marginaux, écologiquement moins favorables, sont caractérisés par une diversité spatiale et une instabilité temporelle. La sélection dans ces milieux s'effectue dans le but de déterminer l'aptitude à la colonisation et la capacité d'adaptation à toute une gamme de facteurs non liés à la densité. La dérive génique centripète de ces zones marginales au moment où les populations se concentrent en petits groupes augmente la diversité génétique du noyau de population, où la sélection favorise généralement les facteurs liés à la densité. En conséquence, la diversité génétique du noyau est améliorée et enrichie. Des études réalisées avec divers organismes révèlent que ce sont les espèces s'adaptant le mieux à divers milieux qui présentent une plus grande diversité génétique. Les populations marginales révèlent une grande importance au niveau de l'adaptation pour l'espèce dans son ensemble, et la protection, la préservation et la gestion des habitats marginaux constituent l'une des « meilleures » stratégies pour maintenir la diversité génétique et les populations des espèces de poisson. C'est donc dire que ces habitats marginaux sont indispensables quant à la diversité et la capacité d'adaptation des poissons.

Introduction

The need for conservation of fish genetic resources has been recognized by fishery scientists and aquaculturalists for some time (FAO 1981). While there is no "best" approach or justification, preservation of marginal habitats with marginal populations is one tactic.

Soulé (1973) has reviewed the general understanding of the genetic structure of marginal populations, and summarized some of the early literature and concepts. There is an absence of fish examples in this literature, so it is necessary to consider the situation by reference to other groups of animals.

It is now generally recognized that small, marginal populations are the mainspring of all ongoing evolutionary change (Mayr 1967, 1982); large, central populations, in which selection usually favours density-dependent factors, are not the arena of ongoing evolution.

I will develop a general conceptual model which stresses the importance of marginal populations for the maintenance of genetic diversity and novelty. Since the existence of marginal populations depends on the existence of marginal habitats, it is obvious that these habitats are needed in order to maintain this genetic diversity.

I will discuss the genetic structure of populations and our current concepts of the importance of marginal populations by considering in sequence the following four main items:

1) Carson's (1958) study of the population genetics of *Drosophila robusta*;
2) Remington's (1968) review of the importance of the genetic structure of populations and insect introductions for biological control;
3) The genetics in small populations, and recent research by Bryant et al. (1986) on bottleneck houseflies; and
4) The general hypotheses of centripetal processes in population fluctuations, as summarized by Brown (1957) in his thesis of centrifugal speciation.

However, before discussing these, it is important to define a marginal population.

Marginal Population

Soulé (1973) pointed out that it is difficult to define a marginal population. He preferred a dynamic definition, which described a marginal population as one characterized by relatively great fluctuations in numbers and a relatively high probability of extinction.

Soulé (1973) pointed out that such marginal populations are not always peripherally located in the distribution of a species; also, that not all peripheral populations are ecologically marginal.

I prefer to define a marginal population as one that is ecologically marginal, small, and usually subject to an extreme of one or more relevant environmental variables, which occur in conceptually "hard" habitats for survival. In contrast, habitats without such extremes are conceptually "soft" and their inhabitants may be regarded as ecologically centrally located. With these definitions, it is possible to discuss the importance of marginal populations and marginal habitats in the context of the maintenance of genetic variability within a species.

Marginal Populations and Marginal Habitats

Population Structure in *Drosophila robusta*

Drosophila robusta is a large, dark-coloured fruit fly that occurs in the eastern deciduous forests, and breeds on sap exudates of a number of trees, principally the American Elm (*Ulmus americanus*). Carson (1955a, 1955b, 1956) studied the genetic structure of marginal populations of this species, and in 1958 (Carson 1958) summarized differences between marginal and central populations. He found 18 different types of gene arrangements within the range of this species, and while most inversion types were widespread, there was a distinct difference between central and marginal populations. While central populations had 6–9 inversion types, marginal populations had only 0–5 inversion types. Near the centre of the range, more than 95 % of females in populations were heterozygous, whereas one marginal population was completely homozygous. In Carson's (1958) view these data showed that central populations were genetically more specialized, many genes being effectively tied up in nonrecombining co-adapted groups. Marginal populations on the other hand, tended to be structurally homozygous, but had greater free recombination. Marginal populations were thus more flexible in the sense of having a greater capacity to adjust to major changes in new conditions.

Ecologically marginal populations also have fewer inversions than central populations of *Drosophila willistoni* (da Cunha et al. 1959). Tabachnick and Powell (1977), pointed out that marginal populations with fewer inversions should be better able to survive new stresses by virtue of their greater genetic flexibility, and have tested this hypothesis. They exposed both monomorphic and polymorphic laboratory populations of *Drosophila willistoni* to chemicals added to the medium. They specifically chose proprionic acid, NaCl, KI and $CuSO_4$ not present in the basic medium in order to minimize the possibility of any population being preadapted to tolerate a particular stress. They showed conclusively that the monomorphic marginal populations adapted to these various media conditions rapidly, whereas the central polymorphic populations did not.

Lewontin (1974) reviewed the data from studies on population structure in *Drosophila pseudoobscura*, and stressed that Carson's generalization about the genetic structure of marginal populations is true if it is ecologically marginal populations rather than geographically marginal populations that are being considered. Lewontin (1974) emphasized the temporal instability in marginal or "hard" environments, and noted the importance of recombination in marginal populations to produce combinations of alleles that are not represented in the "soft" habitats. I would add to this the fact that ecologically marginal habitats are characteristically spatially diverse, as well as temporarily unstable. Such "hard" habitats thus select for different genotypes in different marginal areas. Further, Tabachnick and Powell (1977) have noted that adaptation to marginal habitats need not evolve in an identical manner in all situations. This diversity in response is an important attribute.

Genetic Structure of Populations and Insect Introductions

The establishment of populations of natural enemies for biological control purposes has met with limited success (Force 1967). Remington (1968) considered this problem and observed that the genetic structure of the source population could have a profound effect on the success. He drew a sharp distinction between the success of a colonizing source drawn from marginal populations compared with the lack of success when drawn from central populations. Remington (1968) used the term "marginal" to mean a subpopulation near the environmental limits of a species' distribution. He noted that these were typically small, inbred units with high homozygosity, whereas ecologically central populations are populous, outcrossed units with high heterozygosity.

Remington (1968) noted that in marginal populations selection is for colonization ability and adaptation to a diverse array of density-independent factors. He developed a model that is relevant to the present discussion, because he predicted that the best potential for survival and development of a new, well-adapted, polytypic, introduced population will come from marginal populations.

His model of the influence of the source population on the probable success of an introduction is summarized in Fig. 1. The importance of marginal populations with genotypes for survival and rapid development of new adaptive types is the feature I wish to emphasize.

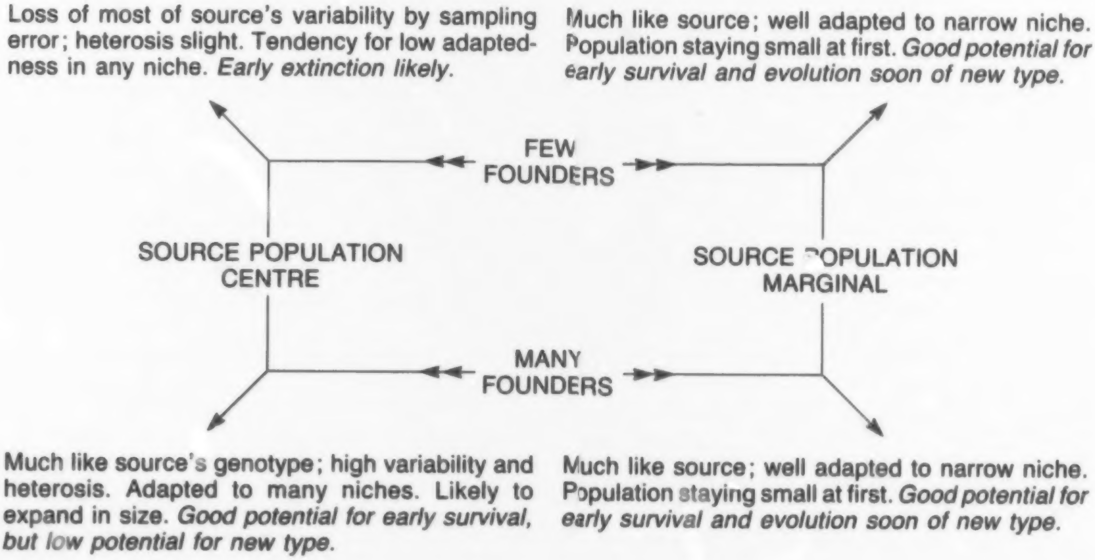
Small Populations

Remington (1968) included the fact that marginal populations tend to be small and inbred. Until recently, it has been assumed that small populations are not very fit, because of the consequences of inbreeding, genetic drift and random fixation (Mayr 1963). Wright (1951) emphasized that fluctuations in gene frequencies in small, completely isolated communities rarely if ever, contribute to evolutionary advance, but merely to trivial differentiation, or in extreme cases to degeneration and extinction.

The best evidence for drift and random fixation in small populations comes from the study of blood group frequencies and other characters in human populations. Birdsell's (1950) study among neighbouring Australian aborigine tribes, Glass's (1954, 1956) study of the Dunkers and Hutterites in North America, and Cavalli-Sforza's (1969) analysis of the inhabitants of villages in the Upper Parma Valley in northern Italy, are the ones most often cited.

Recent analysis of the genetic structure of East and South African populations of the cheetah (O'Brien et al. 1985, 1987) has suggested that genetic drift and random fixation in small populations have brought this species close to extinction.

O'Brien et al. (1985, 1987) have used electrophoretic analyses to demonstrate that the extant populations of the cheetah are even more genetically uniform than inbred laboratory mice. So genetically uniform are they that completely unrelated individuals within the South



Loss of most of source's variability by sampling error; heterosis slight. Tendency for low adaptedness in any niche. *Early extinction likely.*

Much like source; well adapted to narrow niche. Population staying small at first. *Good potential for early survival and evolution soon of new type.*

Much like source's genotype; high variability and heterosis. Adapted to many niches. Likely to expand in size. *Good potential for early survival, but low potential for new type.*

Much like source; well adapted to narrow niche. Population staying small at first. *Good potential for early survival and evolution soon of new type.*

FIG. 1. Influence of the characteristics of the source population on the probable nature of the evolutionary outcome (after Remington 1968).

African population can accept skin grafts without immunological rejection (O'Brien et al. 1985). The genetic homogeneity results in poor breeding success in captive animals owing to the low quality of males' spermatozoa. There is also very high infant mortality and low resistance to disease.

It would seem from these examples that small marginal populations are doomed. However, a recent experiment by Bryant et al. (1986) on houseflies has shown quite the reverse. They found that the three populations of flies bred from 1, 4 and 16 male-female founder pairs showed an increase, not a decrease in variance compared with the ancestral population from which the founders were drawn.

It seems that most of the theoretical models for small populations were based on the notion of additive variance. It now seems that, at least in the case of the houseflies, we might be dealing with non-additive epistatic variation (Goodnight 1987). It is quite possible that there is a shift in what individual alleles are doing with respect to regulatory processes in development. This proposition is very similar to the proposal put forward some years ago by Carson (1968, 1975) when trying to explain the extraordinary variation in the 500 or so species of picture-winged *Drosophila* in Hawaii, that seem to have arisen from one or two founder individuals.

Carson (1975) proposed that there are two separate operational genetic systems within a diploid species, an "open" system and a "closed" system. The "open" system is the one that is freely available to natural selection in large populations, and fosters slow, accumulative changes. In contrast to this, the "closed" genetic system consists of blocks of genes forming co-adapted, internally balanced gene complexes that are not normally subject to expressed variation and selection.

Carson (1975) proposed that founder effects, bottleneck effects, drift and inbreeding in small populations result in complete genetic upheaval and the disruption of the normally "closed" genetic system. The result is a whole new type of variation, with selection being radical and fast. The outcome is the development of new types not possible through selection on large central populations. It is this type of marginally localized process that may be the mainspring of ongoing evolution in diploid species. Indeed, Mayr (1967, 1982) stated that all of the action is in the small, marginal populations.

Centripetal Processes in Population Fluctuations

How are novel and adaptively flexible genotypes in ecologically marginal populations relevant to the ongoing success of a species? Here, I rely on part of the hypothesis outlined by Brown (1957) in his ideas on centrifugal speciation.

Brown (1957) hypothesized that the maximum range attained by a species over an indefinite period of time includes areas favourable and also unfavourable for its continuous breeding and increase. Within the maximum range, the population of a species normally undergoes successive expansions into less favourable, ecologically "hard" marginal areas, alternating with contractions into more favourable, central "soft" refuges. The expansions and the contractions are the consequences of regular density fluctuations.

The result is that the genetic innovations produced in the marginal "hard" habitats can be incorporated into the central population, thus enhancing its genetic variability. In fact, it is only in this way that the central population can incorporate genetic novelties.

Current evolutionary theory on quantum speciation (Grant 1971, 1977; Scudder1974), quantum evolution (Simpson 1944) and switch evolution (Mayr 1967), now being integrated with Eldredge and Gould's (1972) hypothesis of punctuated equilibrium (Stanley 1979), stresses the overwhelming importance of small, marginal populations. Marginal populations are invaluable for the maintenance of the genetic diversity of species.

Marginal Populations, Marginal Habitats and Genetic Resources in Fish

Study of the Sonoran topminnow, *Poeciliopsis occidentalis* (Vrijenhoek et al. 1985) has shown that geographically peripheral Arizona populations contain substantially lower levels of genetic variation (heterozygosity) than do Mexican populations near the centre of the species' range. Hence populations of this fish clearly respond differentially to the differing selective forces in geographically peripheral and central populations.

Although there appear to have been no definitive studies aimed at determining the genetic structure of ecologically marginal versus ecologically central populations in salmonid species, there are a number of studies that show that salmonid populations are spatially variable (Allendorf and Utter 1979; Allendorf and Phelps 1981; Northcote 1981; Northcote and Kelso 1981; Kelso et al. 1981; Parkinson 1984; Wilmot and Burger 1985; Hindar et al. 1986; Crampton and Utter 1987). Indeed, salmonids are characterized by a tendency to evolve genetically divergent local populations (Hindar et al. 1986), and adaptive differentiation may occur on a small geographic scale (Parkinson 1984).

Salmonid species have the potential to evolve adaptations to local environmental conditions (Parkinson 1984), even though selectively neutral mutations, genetic drift, and genetic exchange between populations, rather than selection, can also produce local differences (Aspinwall 1974; Allendorf 1978; Allendorf and Phelps 1981). Marginal populations are likely to be subjected to an extreme of one or more relevant environmental variables. They will, given appropriate conditions, respond by evolving appropriate genotypes.

It is these genotypes that need to be preserved for the future, both with respect to the conservation of the genetic resources of these fish species, and the survival of the species itself (FAO 1981).

Marginal habitats often support only small populations of a species. It is true that in some cases these small numbers can lead to inbreeding depression and loss of fitness (Allendorf and Utter 1979; Kincaid 1976a, 1976b; Kosswing 1973). However, it is in these marginal populations that unique adaptive traits are to be found. They need to be preserved. Marginal populations of fish are a valuable asset for the future.

Marginal habitats must be maintained, preserved and managed to ensure the survival of such marginal populations. I argue that it is one of the "best" ways to conserve the genetic resources of fish species.

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Report of the Working Group on Methodologies for the Quantification of the Effects of Habitat Alteration on Yield

Chairman: P.J. LeBlanc

Rapporteur: D.J. Meerburg[1]

Participants: M. Henderson K. English D. Ryder
R. Reisenbichler T. Whillans B. Schuter
P. Delaney T. Webb B. Masse

This Working Group session investigated the methodologies currently in use or available for the quantification of the effect of habitat alteration on fish yield. During review of the papers presented in the Methodology session, it was evident that it is often extremely difficult to determine the effects of habitat alteration on adult salmonid yield. Some specific habitat alterations can be assessed as to their impact on specific freshwater life stages of salmonids. However, there is difficulty extrapolating to the ultimate effect on adult yield due to the many intra- and inter-specific stock interactions which may take place during marine life as well as interannual variability in the physical and chemmical characteristics of the marine environment. For example, a habitat alteration which reduces the number of juvenile salmon in freshwater by 50 % may also lead to larger average sizes of smolts produced (due to increased food availability). These larger smolts may survive at twice the average rate and adult returns may be unaffected.

Session participants noted that, prior to considering the effects of habitat alteration on yield, one needs a better understanding of the effect of habitat on yield; the habitat must be quantifiable and its relation to fish productively understood before consideration can be given to what the impact of altering the habitat will be. This is obviously relevant in relation to the DFO policy of "no net loss". If the amount of habitat and its productive capability is not known in the first place, it is not possible to determine options to maintain production if the habitat is going to be altered.

Session participants encouraged the use of innovative statistical techniques, such as the "staircase" experimental design proposed by Walters et al. (this volume) to control for time-treatment interactions. Reasons for such approaches were brought to light in the paper of Bledsoe et al. (this volume) where it was shown that even large changes such as ± 50 % in estimated population size in Pacific salmon stocks are difficult to detect over time using conventional statistical techniques.

Rather than trying to review habitat methodologies used in each region of DFO, the session participants concentrated on activities and processes common in all regions. The consensus was that DFO should be, and is currently, dealing with fish habitat on various levels, the three main ones being:

1. The "small impact" project level.
2. The "large impact" project level.
3. The synoptic level.

The "small impact" project level involves the referral system of DFO. Referrals from other agencies serve notice of small projects being conducted by other agencies (e.g. Public Works) or private companies and therefore capture the high frequency pertubations to fish habitat. DFO response is usually at the fishery officer or habitat management officer level, dealing with situations such as culvert placement, timber harvest, and gravel extraction. Assessment methodologies for these small projects were weak and non-standard. Further, the level of change in fish yield from any one small project may be so small as not to be measurable.

The "large impact" project level involves the larger scale projects which by themselves have the potential to significantly affect fisheries habitat (such as the recent Nechako River issue in British Columbia). These projects usually require considerable resources for assessment purposes, both before and after project implementation. Often teams of DFO biologists and engineers and outside consultants are required. Assessment methodologies for this level of activity are more complex than those of the "small impact" projects and can involve more detailed models such as HEP (Habitat Evaluation Procedure) and Instream Flow Incremental Methodology (IFIM) (see Shirvell, this volume).

The "synoptic" level is an intensive research approach where projects are planned and of a long-term nature. Such projects are designed to provide answers applicable in other areas and are useful in the development of "rules of thumb" for use by field personnel at the "small impact" project level. These synoptic studies are essential for DFO to be able to address the day-to-day habitat issues such as referrals.

The main difficulty noted with the three different categories or levels of habitat activity indicated above was the lack of integration between the levels. The Session

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participants agreed that more effort will be required in the future communicating the results of activity at any one of the levels to personnel working on projects at the other levels. In general, the flow of information for management should be from the research projects to the large scale and referral levels, thus emphasizing the role of technology transfer.

The session concluded with the following recommendations:

1. Methods needs to be designed to meet different levels of DFO activities.
2. As most of DFO's activities are habitat referrals at the fishery officer or habitat manager levels, information of the form of ''rules of thumb'' must be provided to these staff. This will lead to standardized methodologies (to the extent possible) for response to referrals.
3. Well designed large-scale synoptic programs need to be in place to measure the long-term impact of habitat alteration on fish yield.
4. Better procedures need to be in place to transmit information from the small ''referral-types'' projects to the synoptic level and vice-versa.
5. A rating scheme to measure the amount of habitat and its productivity must be in place.
6. Consideration should be given to adopting a decision model developed by Ducks Unlimited to fisheries/habitat problems.
7. Decision support systems (decision trees — ''expert systems'') need to be developed for use at the referral level.
8. Large scale projects need more ''post-evaluation'' to calibrate predictive models.
9. Better screening processes need to be implemented to determine which projects require detailed assessment/evaluation.

Report of the Working Group on Physical Effects on Salmonid Stocks

Chairman: L. Dominy

Rapporteur: J.S. Macdonald[1]

Participants: D.A. Levy, J. Payne, V. Poulin, G.H. Reeves, C. Scrivener, R. Ptolemy, J.C. Davis, A. Solloff, I.V. Williams, H. Rueggeberg

The following issues, from four major industrial areas, were identified as frequently having a physical effect on fish habitat in Canada:

a) Forestry
  - timber access roads
  - felling and tree removal
  - estuarine log storage

b) Mining
  - placer mining
  - low stream flows resulting from industrial water requirements
  - stream diversions

c) Agriculture
  - irrigation induced low flows
  - channelization and diversions
  - soil loss into aquatic systems

d) Energy
  - hydroelectric dams
  - cooling water intake and discharge
  - tidal power

Examples of multiple resource use conflicts by the agricultural, forestry and other estuarine users were presented by the Working Group members. Loss of fish production due to salmonid habitat loss in western North America has been occurring at least since the early part of this century (e.g., Lichatowich, this volume). Multiple resource use has been increasing but our ability to regulate industry and impose environmental protection standards has also increased. Our ability to regulate industry is due partially to our increased knowledge of the resource. During this session alone, we have seen examples of: (a) the importance of estuaries to the survival of juvenile chinook salmon (Levings et al., this volume), (b) the negative effects that water diversions can have on the survival of salmon outmigrants (Kjelson and Brandes, this volume), and (c) the variability in the effects on chum and chinook survival of clearcutting and log storage activities (Holtby and Scrivener and Levy et al., this volume).

Much of our habitat research success is due to the adoption of a multi-disciplinary approach as mentioned by Beamish in his opening remarks. In addition to the disciplines of terrestrial ecology, geomorphology and hydrology which are frequently contributing to habitat research, it is essential that our research incorporate other disciplines such as landscape ecology and paleoecology if we want to again a full understanding of how physical alterations influence salmon populations.

With the advent of the Department of Fisheries and Oceans habitat policy of no net loss and in some cases a net gain it has become increasingly important to be able to describe habitat types in terms of the capacity for salmon production. This requires a knowledge of the habitat features that limit the production potential of each life stage. Our ability to defend management decisions and to design restoration projects depends on this information.

Clearly, fish production losses, as they relate to every possible type and every possible degree of habitat perturbation cannot be calculated for every fish rearing habitat in Canada. Effective habitat management requires extrapolation from research results in one area to predict results of perturbations elsewhere. However, application of results from a few studies within a limited geographic or physiographic region cannot be justified on scientific grounds given our current state of knowledge. Our ability to predict will improve with increased knowledge of both environmental variables and fish stock susceptibility in different locations. Therefore, future research should incorporate the following points if we are to develop timely information that will be useful to fisheries managers:

a) Short-term studies should be developed to identify significant environmental variables in various biogeographic zones.

b) A classification scheme should be developed that defines regions or habitat types in terms of their most significant environmental variables.

c) In British Columbia we need a better understanding of the differences in the adaptation of specific stocks to their environment (e.g. coastal vs interior — Swales et al. 1986, Tschaplinski and Hartman 1983). The effects of altered habitat on fish stocks varies with location. This will require more sophisticated techniques for stock identification particularly during the adult life phase.

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A portion of our research budget must be devoted to long-term studies. Long term trends cannot be predicted from short-term environmental changes. It is only through data on long-term trends that we will know if habitat alterations have had an effect on salmon production. However, long term data bases, such as those collected using and intensive before, during, and after perturbation approach can be quite costly and will provide information that applies to only one region. The work can be made more cost-effective if an experimental management approach is adapted. The researcher can then take advantage of preplanned environmental impacts by examining the habitat where an alteration is about to occur (Wilimovsky — keynote address). The costs of the experimental alteration and much of the data collection may be covered by the organization that is, for example, removing timber or constructing dams. Alternatively, development of data bases from extensive post treatment analysis (e.g., Hall et al. 1978 — short-term, synoptic experiments in watersheds with varying logging histories), or from literature surveys can take less time and cost less money than "before and after" style experiments and still yield information regarding long-term changes due to habitat alteration. Ultimately we cannot rely on any one type of approach but must use a wide variety of short- and long-term study approaches to increase our understanding of the effect altering habitats has on fish production.

Many habitat models have been developed in an attempt to better describe, predict or extrapolate physical and biological changes. To date these models have been used successfully to isolate physical variables important in documenting habitat alteration or in describing fish habitat. They have been less successful for prediction or extrapolation (Shirvell, this volume). Habitat modelers may want to consider the following points:

a) There must be greater consideration given to correlation among the independent variables used in the models. Variables which are highly correlated contain similar information. With the use of multivariate techniques, the identification of intervariable correlation allows data matrix reduction and simplification. Correlation among variables often has more biological meaning than the variation of the variables themselves. For example fish exposed to high levels of competition are often more succeptible to diseases. Therefore, competition levels affect survivorship through stress and disease levels (Reeves et al. 1987).

b) Variables frequently do not interact in a linear fashion. At given levels certain variables may interact synergistically such that the overall effect of their interaction in a biological process is greater than the sum of their separate effects. The effect of low stream flows on anadromous fish survival depends not only on the degree to which flows will be reduced but also on the temperature during the season in which the flows will be reduced. Hence the potential effect of a variable is not only dependent on its own level but is also dependent on the levels of the surrounding variables (cumulative effects). For example one timber sale may have a positive effect on fish stocks in an adjacent stream but two or more sales or a clear cut may cause chronic damage. Additionally, the pattern of disturbances (alternating patches of pristine and perturbed habitat) may be more important than the amount or type of damage itself. Some day it may be able to minimize environmental damage through optimizing the distribution of impacts in a manner which conforms to the natural, 'patchy', distribution of our fish populations.

c) Many habitat models are based solely on physical habitat parameters. The incorporation of biological parameters such as risk of predation, degree of competition or potential feeding success would yield more realistic models that presumably will have greater utility for both researchers and managers. We must also be aware of what it is we are trying to optimize. For instance the importance of a specific habitat cannot always be measured by the amount of time it is occupied by fish (Larimore and Garrels 1985). Infrequently used sloughs may not have the water quality required to support salmonids but may support the marsh vegetation on which the detrital food chain supporting salmon is based. The true value of a model may simply be the act of creating it. Any process that forces us to examine the physical and biological parameters involved in shaping habitats can lead to improved scientific insights. However, dependence on models as a method to quantify and predict habitat relationships while ignoring relevant qualitative information can lead to difficulty. When it comes to evaluating the effects of specific activities on fish and fish habitat, there is no substitute for the informed opinion of the biologist in the field.

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Report of the Working Group on Chemical Effects on Salmonid Stocks

Chairman: J. McInerney

Rapporteur: I.H. Rogers[1]

Participants: D. Seiler, L.B. Holtby, J.A. Servizi, R.W. Gordon, D.W. Martens, I.K. Birtwell, J. Gibson, J.C. Davis, H. Ruggeberg

The Chairman invited Working Group members to discuss habitat problems of interest in their regions.

Pulp and Paper Wastewater Discharges

The Grays Harbor experience in Washington State (Seiler, this volume) is an interesting case in relation to the objectives of this workshop. Here the effects on the population are known but the linkage to a cause is missing. Most often scientists measure the toxicity of a chemical to single or groups of fish in the laboratory. In the 1970's the government forced pulp and paper mills on the estuary at Grays Harbor to install secondary treatment. Although the oxygenation of the receiving water improved, the survival problem for Chehalis River coho stocks relative to Humptulips coho, which also use the estuary, was not solved. Any improvement in recruitment of Chehalis stocks was marginal and indistinguishable because of the lack of precision in the data and the continuing heavy fishing pressure. During the 1960's and early 1970's there was a very high ocean harvest rate of Chehalis River stocks, coupled with an ongoing fishery within the harbor leading to low levels of escapement. The difficulty in "proving" what went wrong after the fact is often immense, as shown by the Grays Harbor Case. A parallel case in B. C. is the unresolved issue of the effects of pulpmill effluent on chum stocks in Neuroutsos Inlet (Birtwell 1988). Scientific experiments cannot directly prove what caused these problems. Hypotheses can be advanced and experiments devised to reject them.

Servizi (this volume) advised of the wisdom of calling for tough measures to control waste releases before permits are granted for the construction of pulp mills that discharge to fish-bearing waters. In the late 1960's the Canadian Department of Fisheries called for the application of state-of-the-art secondary treatment at new pulp mills planned for the Fraser River. The salmon fishery has survived and sockeye and pink salmon stocks are even increasing. The alternative to such regulatory action is intervention to "sort out a mess", as in the case in Grays Harbor or Neuroutsos Inlet.

Beneficial Effects Associated with Nutrient Additions to Salmon Habitat

John Gibson described observations on stream productivity in St. John's, Newfoundland. Some undeveloped freshwater streams flow through the city and still contain healthy populations of brown trout. There is limited angling for these fish. The productivity of rivers in Newfoundland is generally low and the waters are nutrient poor with a short growing season. Average trout biomass in a stream might be 1 $g.\cdot m^{-2}$. However, in a channelized section of a stream in St. John's eight small trout were captured per sq. metre (biomass = 63 $g\cdot m^{-2}$).

Atlantic salmon were introduced into a section of another stream where the measured biomass was 15 to 16 $g\cdot m^{-2}$. Over a two-year period the salmon displaced the brown trout. This was unexpected since, in Europe, brown trout are often removed from streams being planted with salmon. Moreover, a slightly higher biomass was recorded for salmon than for brown trout. This section of stream probably received nutrients from a dairy farm. It seems that nutrient additions to Newfoundland streams could be effective in enhancing salmon productivity, which could have important management implications. Controlled fertilization on the Keogh River on Vancouver Island has resulted in increased salmonid biomass (Perrin et al. 1987).

Past experiences with nutrient additions to salmon habitat in B.C. have sometimes yielded negative results. This was the case on the Thompson River in the 1970's, when nuisance blooms of gelatinous diatoms became prevalent below Kamloops Lake. The cause was found to be the release of phosphorus from the Weyerhaeuser Canada Ltd. kraft mill and the City of Kamloops sewage lagoons. The problems on the Thompson River were deciphered with the aid of controlled experimental streams (Bothwell 1985).

Problems Associated with Secondary Chemicals

A mainstay of the economy in B.C. is the pulp and paper industry with 23 mills, of which 6 discharge to the Fraser River system. Tri- and tetrachloroguaiacols, formed by the reaction of chlorine with residual lignin, are not efficiently destroyed by secondary treatment. Furthermore, recent work in Sweden suggests that chlorolignin itself is chemically unstable and capable of releasing chloroguaiacols by further breakdown after discharge. There may be chemical alteration of salmon habitat, and possible sublethal effects, in the Fraser River due to pulp bleaching. Limited studies have shown the presence of 3,4,5 — trichloroguaiacol and tetrachloroguaiacol in the 100 ppt range in river water samples collected at stations from Prince George to the sea. These compounds bioaccumulate in juvenile chinook salmon that overwinter under ice in the upper Fraser River (Rogers et al. 1988).

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A Need for Better Evaluation Procedures

Great improvements in the detection and quantitation of pesticide residues have resulted from the introduction of improved instrumentation. However, our ability to interpret the significance of low levels of toxicants to the health of fish has lagged. Appropriate techniques are needed to measure the fitness of salmon. One use for such methodology would be to record the current status of salmon stocks subject to future environmental stress from human population growth. Presently we are uncertain which physiological and biochemical parameters would be most valuable to measure.

There is a need for complete life cycle studies, which can evaluate population effects, for example, smolts to adult survival. These long term experiments can only be conducted at selected sites, for example rivers or estuaries adjoining pollution sources such as the Chehalis or Humptulips Rivers in Grays Harbor. In British Columbia, the Rainy River, adjacent to the Port Mellon pulp mill in Howe Sound, might be a candidate. Such studies would be difficult to conduct on the Fraser River because of a mixture of stocks would have to be coped with in the experimental design.

The interactive effects of multiple chemical stressors in an issue that has received little experimental study. Such effects may be additive, synergistic or antagonistic. Experimental design to deal with such issues can be difficult and the net effect may be site specific and dependent on which particular stresses are involved. This matter may be very significant in highly industrialized areas.

The literature provides some examples of new tests that measure the fitness of individual fish, but which have not yet been attempted by DFO. One is the measurement of backbone strength, now conducted routinely at the Columbia National Pesticide Laboratory of the United States Fish and Wildlife Service (Buckley et al. 1985). This was used with other tests to examine the reasons for poor swimming performance of striped bass, hatched in the Hudson River, N.Y., where serious PCB pollution exists. New analytical methods will be required to study the environmental impact of wood preservation chemicals that are now starting to replace the use of chlorophenols in B.C. This may require the purchase of specific instruments and detectors not currently available within DFO.

The Need to Demonstrate Positive Results from Actions Taken

This important consideration is often overlooked. The argument centers on the value of a stock integrated over time, which is its true value. When actions have been taken to coerce a polluting industry to upgrade its waste treatment performance, it is important to measure the resulting improvement in terms of a more stable fish population and an increase in value of the resource. This information can be used to demonstrate real returns to the local economy as a direct result of regulatory action. Without such evidence resource managers will often be accused of simply making bureaucratic decisions, devoid of scientific justification.

Perhaps we should give thought to how things might be from the viewpoint of an industrialist. For example, we could suppose that we were in the position of manager of an industrial operation that has had to upgrade its waste treatment plant. A few years after making such an investment in good faith he is informed that there are still problems that will require the expenditure of further large sums of money. It would be logical for him to ask regulatory agencies to show proof that such an expenditure could solve the problem and that still further outlays might not be demanded a few years later.

The Use of Scientific Inference

Resources are not sufficient to allow scientific studies to examine the potential impact of every development proposal. Thus managers must spend their research dollars where they judge the best returns will ensue, including the need to demonstrate impacts on fish populations. Sound scientific principles and judgement must be used to extrapolate from demonstrated effects on groups of fish at the experimental level to anticipated effects at the population level. By the time a problem has become so serious as to have observable impact at the population level, the resource may be in serious trouble.

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Report of the Working Group on Permissible Levels of Inference in Habitat Management for Salmonids

Chairman: F.C. Boyd

Rapporteur: L.H. Bain[1]

Participants: R.J. Beamish, J.C. Davis, C.D. Levings, C.D. McAllister, R. Morley, A.R. Thompson, M. Waldichuk, H. Waldock

Workshop discussion began by developing a definition of inference as follows: a process of deduction based on limited knowledge. The participants agreed that inference is multileveled — the level being set by the rigor with which the inference is tested or challenged. In science, inference is based on deductive reasoning. Scientific inferences are continuously being tested experimentally and assessed through peer review, and in this sense, are probably the highest or most rigorous form of inference. Unlike other realms in which inference is used, the time frame in which scientific inferences can be challenged is long. Outside the realm of science the gradient of inference, as set by rigor with which it is tested, is law, management and politics in order of decreasing strictness (Thompson and Ruggeberg, this volume).

While the "rigorousness" of inference is highest in science, its permissible level or, its acceptability, in this field may be very low. With the primary objective of "understanding", the acceptable level of inference in science is controlled, as mentioned earlier, by a rigid set of standards and the process of peer review. In this context, scientists hedge on conclusions based on inference. For example, disclaimers are often used when publishing laboratory experimental results which state that the data may not be applicable to the "real world".

The low level of acceptability in science notwithstanding, inferential knowledge is a component of this discipline. Participants pointed to the long range transportation of acid pollutants and their effects on lake pH and lake enrichment as two examples of inference used within the scientific arena. Although absolute proof is lacking the scientific community is in general agreement with the inference that "acid rain" harmfully alters fish habitat. In the case of lake enrichment, inference, based on theory and earlier lake experimentation, suggested that the addition of fertilizer to oligotrophic lakes containing sockeye salmon fry would increase the size of the adult return. Experimental results were consistent with the hypothesis, however, it remains to be proven whether the increased adult sockeye salmon returns were a direct result of nutrient addition. Yet this particular inference was accepted as is evident with the launching of a sockeye salmon lake enrichment program in British Columbia as a means of increasing adult runs.

Within the fields of law, management and politics, the workshop participants saw permissible levels of inference used in the decision-making process as being set by a number of factors. These factors included the objective of the decision, the sociological and economic impacts of the decision from the point of view of both the permanency of the decision and its effect on fish. If the standard of proof in a court of law is "beyond a reasonable doubt", then inference is rarely permissible. On the other hand, where the court is dealing with a "balance of probabilities", inference is used more readily in weighing all the input in order to reach a decision based on reasonable probability. As one participant explained, permissible levels of inference vary along a gradient. Inference occurs at a low level in law depending on the standard of proof required and ascends in inverse proportion to the impact, fish value or consequence of the required decision within the realms of management and politics.

Discussion turned to methods of establishing acceptable level of inference. It was suggested that consensus is, in effect, a recognition of permissible levels of inference. Therefore, the levels of acceptable inference can be established by consensus exercises whether it be peer review in science or consensus goal-oriented exercises used to reach important managerial decisions. Others suggested using decision/risk techniques to assist in evaluating the levels of inference allowable in a particular decision-making process while for science, one participant proposed the use of "science-courts" as a means of setting inference levels. At the extreme end, inference can be institutionalized through the process of legislation (Thompson and Ruggeberg, this volume).

There was a perception among the participants that a double standard exists in judging inferences when the science discipline interacts with those of law, management or politics in fish habitat matters. Scientists' rules regarding the use of inference are strict, whereas those used in other fields are much more flexible. For example, a statement made by an economist or politician regarding the benefits of a particular project is rarely challenged by those affected even though the "proof" of the statement is rife with theoretical projections and inference. On the other hand, scientists are loath to make broad pronouncements based on inference because of the stringent rules they set for themselves regarding its use. Consequently when scientists offer opinions, they are often challenged or come under suspicion because of their general unwillingness to use inferential knowledge in the first place.

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But not all of this apparent double standard can be blamed on different rules by which inference is accepted in a public arena — whether these rules are self-imposed or not. Participants also felt that conflicting values played a large role creating the double standard of acceptability of inference. As was stated during this discussion: "if we are to accept the premise that the use of inference is valid and permissible in the absence of proof, then we as scientists and managers should not be intimidated by the critics who reject decisions made by us using inference. Often these criticisms are based on opposing values and any decision made which does not protect or support these values is challenged".

Finally, the workshop concluded with a general discussion centering on suggestions for action and future needs. The major points of this discussion are listed below:

1. It was suggested that a systematic review of DFO habitat decisions be undertaken where inference has been used. Such a review, it was felt, could assist DFO scientists and managers in better understanding the role of inference in fish habitat-related decision making.
2. In the process of decision making, those decisions based on science and technological factors should be kept separate from decisions based on values.
3. There is a need to eliminate the double standard applied to scientific inference by those who use inference themselves in decision-making.

Closing Remarks

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Present Situation

In DFO the Department has undergone considerable change as a result of science integration and reorganization. Science integration has combined our oceanographic expertise in the physical and chemical sciences with our biological expertise allowing us to adopt a multidisciplinary approach to research and problem solving. I think this will be a major advantage to us for the future in allowing us to focus the diverse talents of our scientists on important issues including fish habitat.

In addition, we have embarked upon a new habitat policy in the Department that encompasses the concepts of no net loss and net gain. This initiative means that it is essential that we try to come to grips with measuring the productive capacity of habitat in terms of fish production in order to be able to implement the policy. Inevitably, we shall be involved in multiple resource use conflicts where social, economic and biological considerations are at issue and the value of fish-producing habitat is the subject of debate. In B.C., the matter of salmonid production is a critical and highly visible issue leading to great public concern with respect to habitat issues and one can expect this concern to intensify as development proceeds and related issues such as Native claims become more prominent.

Furthermore, we find ourselves in a climate of budgetary restraint and deficit reduction and fisheries and ocean specialists both in Canada and the USA are facing an ever-expanding workload with scarce financial and personnel resources. This means that we must focus those resources on our highest priorities where we get the best results and that our research effort must be directed to key problem areas. While we face a difficult challenge and the matter of assessing the productive capacity of salmonid habitat is particularly complex, I think it is important that we look at our efforts in a historical perspective. Fisheries biology and habitat assessment is really only a very young science and I think you can agree that we have come a long way in a relatively short time.

Programs are being developed which should start to help us unravel the mysteries of marine survival and recruitment of salmonids and developments in this area should help us pinpoint critical stages in salmonid life history. A better understanding of marine survival should help us focus on the relative importance of habitat concerns in relation to the life cycle and better define critical events related to recruitment and population size.

Finally, I think we must recognize that we are working in a time of increasing challenge, both in a legal sense and from a scientific and technical perspective. Indeed, our advice and conclusions will be subject to increasing scrutiny and our task is to provide the best objective scientific assessment possible that can stand the test of peer review and challenge. Obviously, we will never have all the facts and we cannot wait for completion of exhaustive studies in many circumstances, thus highlighting the importance of our discussions this week.

Our Approach and the Interrelationship of Methodology

A most important task for us is to determine how best to focus the talents of the biologists, chemists, toxicologists, ecologists, habitat managers, oceanographers, and fisheries enforcement personnel in order to protect and improve the resource. This means that communication, planning, priorization of tasks and coordination are important as well as the educational aspects of sharing results, conclusions and proven approaches. It is very important for us to attempt to measure the value of fish habitat in terms of fish production, survival, recruitment effects, thus the prediction of overall population impact of habitat loss or gain becomes a major objective. We need to understand how ecosystem, community or habitat characteristic changes are good or bad from a fish production perspective and how small or large changes affect production. We could profit from devoting more attention to statistical and logistical approaches by defining what types of habitat require study, assessing the portability of results from location to location and defining how we can or cannot extrapolate findings from one site to another. In essence, do we have to study each problem on a site-specific basis or can we learn from detailed case studies and apply our results elsewhere?

Methodology has been an important topic in your discussions this week and there would appear to be consensus that increased emphasis on statistical methods, multivariate analysis and the need to separate the "noise" from measurable effects is a major challenge. Furthermore, methods of stock identification, use of coded wire tags, the development of new stock identification procedures such as DNA analysis and methods of measuring abundance, survival and population trends would appear to be essential elements in addressing this issue. It is important that we try to find "indicators" which guide us as to the "health" of a given situation and state of the habitat. Are there chemical and biological tests that serve as indicators to guide us and what utility exists in modeling and the assumptions contained therein? Finally, we know very little about the effects of multiple stressors — mixtures of chemicals or combinations of toxic stressors and physical and chemical features of the environment. This is a topic urgently in need of more study and attention.

The Scale of Habitat Problems Encountered

Fisheries and habitat managers and environmental agencies face a huge array of issues from very large-scale projects with possible major habitat effects to many small-scale effects. A very considerable workload exists in the habitat referrals area with literally thousands of referrals facing us in a given year. Obviously, our response has to be different for a large-scale project compared to a small one, yet there is a real danger of losing a significant amount of habitat through the additive effects of accumulated minor disruptions. This means that it is very important for us to categorize habitat issues by type of disruption, develop guidelines for fisheries officers and field personnel to employ in the field, and communicate recent results to personnel dealing with the referrals process. Again, communication, education and coordination of effort would appear to be crucial in allowing regulatory agencies to cope with the workload in the most effective manner.

The Criticality of a Given Habitat Effect or Timing

A factor that can sometimes get overlooked in our response to habitat concerns relative to the salmonids is the relationship of habitat utilization to the life cycle and migratory behavior of the fish. Rearing and spawning areas crucial to growth, vigor and reproductive success are undoubtedly different from areas utilized for shorter periods of time for fish passage during migration. Salmonids exhibit the ability to utilize avoidance behavior in stressful circumstances or may utilize given habitats only at specific time periods or for a very brief duration. Thus it seems essential that we be able to relate our approach to habitat protection to an assessment of the criticality of that particular situation in terms of the life cycle of the salmonids in order to development meaningful and effective assessments.

Application of Knowledge for the Future

In summary, some key issues that must be addressed would appear to be:

— Is each situation site-specific or can we apply results of detailed studies to other situation and extrapolate our findings?

— How do we measure habitat effects and separate the "noise" from measurable changes and quantify such change?

— Can we tackle the difficult problem of describing habitat effects in terms of quantitative effects on salmonid populations and what approaches/methodologies will facilitate progress?

— How can we assess the results of our approach to habitat protection? It would seem most useful to try to learn from experience by following up and examining results of our interventions after the fact and document the effects of those interventions.

— What approaches can we adopt in order to translate knowledge into action in terms of regulatory success, legal action, public and private sector knowledge, environmental review methodology and in terms of working with the private sector?

THANK YOU

Acknowledgments

We would like to acknowledge Dr. R.J. Beamish, Director, Biological Sciences Branch, Pacific, for stimulating the workshop and for delivering a cogent welcoming address to help set the tone of the meeting. Dr. Mike Healey, Pacific Biological Station, assisted in the formative stages of planning the workshop. At the Workshop banquet, held on the evening of May 7 at the Coast Bastion Hotel, Dr. N.J. Wilimovsky, University of B.C., gave a very thought provoking and entertaining talk, recounting some of his experience in fish habitat management. This has ranged from dealing with the Aleyska pipeline issue in Alaska to problems with the accidental capture of tropical porpoises. The group benefited from his review of these major projects. Dr. J.C. Davis, Pacific Region Director, Science, gave a thorough summary of the proceedings at the conclusion of the Workshop and we are grateful to him for this paper. All papers in these Proceedings were subjected to anonymous peer review and we are grateful to the referees who assisted with this task.

Abstracts of Papers Given at the Workshop but not Submitted for Publication

Effects of Lake Acidification on Salmonid Populations

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The primary mechanism for population losses of lake salmonids due to acidification is apparently successive recruitment failures. The exact life stage where increased mortality occurs has not been conclusively identified. Field thresholds for population losses vary between salmonid species and synoptic surveys appear adequate for defining these thresholds. Most studies indicate that losses are due to direct toxicity rather than to changes in food webs, but recent studies indicate that this latter mechanism may contribute to losses. While there are many field studies that document losses of salmons and trouts from lakes, there are fewer for chars, and very few for ciscoes and whitefishes.

Sources of Variation in Responses of Juvenile Sockeye Salmon (*Oncorhynchus nerka*) to Addition of Inorganic Nutrients to British Columbia Coastal Lakes

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Addition of nitrogen and phosphorus fertilizer to oligotrophic British Columbia coastal lakes has resulted in general increases in autotrophic and heterotrophic production and frequent increases in standing stocks of zooplankton. These changes at primary and secondary trophic levels have been reflected by a number of positive responses by juvenile sockeye including: increased lacustrine growth, increased lacustrine survival and associated increases in the size and abundance of outmigrant smolts. Positive responses have not been readily identifiable in some lakes and years due to exceptional conditions. Examples of the latter include: (i) responses to treatment by large net phytoplankton which likely do not enter the food chain leading to sockeye salmon; (ii)) responses to treatment by sockeye competitors such as limnetic sticklebacks (*Gasterosteus aculeatus*) that reduce the flow of food-energy to juvenile sockeye and (iii) lakes producing enough zooplankton in an untreated state so that sockeye growth is apparently not food limited. Although we have made considerable progress in defining the range of responses to expect from juvenile sockeye in lakes undergoing controlled eutrophication our understanding of the factors controlling the interrelationships between different trophic levels among groups of lakes is still too crude to invariably predict the frequency, direction or precise magnitude of response by sockeye salmon stocks.